THE CYTOLOGY OF *PAPHIOPEDILUM MAUDIAE* HORT.[1]

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Statement of the Problem

The hybrid *Paphiopedilum Maudiae* Hort. is the offspring of *Paphiopedilum callosum* var. *Sanderae* and *P. Lawrenceanum* var. *Hyeanum*. It has been used in relatively few crosses despite its quality, and its offspring have rarely, if ever, been able to exceed it. It was felt that an orchid of such superiority which produced little and often no seed should be examined cytologically to ascertain, if possible, the causes of its sterility. Accordingly, cytological examination was made of the parents and the hybrid and some observations were made on somatic tissues of certain related species.

I. Paphiopedilum Pfitz.

Paphiopedilum was originally incorporated in the genus *Cypripedium* described by Linnaeus. From *Cypripedium* were later extracted the three other genera of the Tribe Cypripedilinae as they are generally accepted today; the residue of the large genus continues under Linnaeus' original designation. The orchid-grower continues to refer to various species of *Paphiopedilum* as "*Cypripedium*," and the confusion oftimes extends to the remaining genera.

Linnaeus arrived at the name *Cypripedium* in an effort to latinize what he thought were the proper Greek words for the "Slipper of Venus." These are Κυπρις (Latin *Veneris*) and ποδιον *(calceus)*. The last, however, does not signify the Latin *calceus*, or shoe, but rather is the word for a small foot. Ascherson[2] changed the generic name to *Cypripedilum* (*pedilum* representing the latinization of the Greek equivalent of *calceolus*), and this was adopted by Pfitzer (1886) and published as such. Buser (1894) has concluded that both names represent the latinization of "very mediocre Greek," but that by virtue of priority *Cypripedium* would be correct. Since Linnaeus had used *Cypripedium* consistently in both 'Species Plantarum' and 'Genera Plantarum' Pfitzer would have no right under present-day rules to suggest a change.

Selenipedium was changed to *Selenipedilum* by Pfitzer in 1886 on the same basis that the change was made in *Cypripedium*. The genus was originally described as *Selenepedium* by Reichenbach filius (1859) who used this spelling consistently. On the basis of priority as determined by the present-day rules of nomenclature, *Selenipedium* is the proper expression.

The use of *Phragmopedilum* rather than *Phragmopedium* suggested by Rolfe (1896) is mandatory today since the genus was published originally as *Phragmopedilum* by Pfitzer. In the same manner *Paphiopedilum* (rather than *Paphiopedium*

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[1] An investigation carried out at the Missouri Botanical Garden and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Henry Shaw School of Botany of Washington University.

[2] Ascherson, P. Flora d. Prov. Brandenburg, p. 700, *in nota*. 1864.

of Kerchove, 1894, or Rolfe, 1896) takes precedence. The regularity that Rolfe sought for the endings of the generic names within the group, and the change sought by Pfitzer on the basis of derivation are tempered by priority. The following keys to the genera, with necessary modification to generic names, are taken from Rolfe and Pfitzer in that order and are offered for comparison.

ROLFE'S KEY TO ORCHIDEAE (ORCHIDACEAE OF PFITZER)

Suborder DIANDRAE (PLEONANDRAE of Pfitzer)
Tribe CYPRIPIDIEAE (CYPRIPEDILINAE of Pfitzer)
Ovary 3-celled with axile placentas; sepals valvate.
Leaves plicate; perianth persistent; seeds subglobose.....*Selenipedium* Rchb. f.
[3 species in South America and Brazil]
Leaves conduplicate; perianth deciduous; seeds fusiform.....*Phragmopedilum* (Pfitz.) Rolfe
[11 tropical American species]
Ovary 1-celled with parietal placentas; seeds fusiform.
Leaves plicate; perianth persistent; sepals valvate.....*Cypripedium* L.
[about 30 widely scattered species in Europe, temperate Asia, and North America]
Leaves conduplicate; perianth deciduous; sepals imbricate.....*Paphiopedilum* Pfitz.
[46 species in tropical Asia]

PFITZER'S KEY TO ORCHIDACEAE

PLEONANDRAE
Tribe CYPRIPEDILINAE
A. Vernation of the leaves convolute, perigonium marcescent, persisting in the fruit.
a. Ovary trilocular, seed almost spherical with brittle outer coat....*Selenipedium* Rchb. f.
b. Ovary unilocular, seed elongate with fragile coat.....*Cypripedium* L.
B. Vernation of leaves duplicate, perigonium deciduous.
a. Ovary trilocular, vernation of sepals valvate, margin of slipper-shaped labellum broadly involute or induplicate.....*Phragmopedilum* (Pfitz.) Rolfe
b. Ovary unilocular, vernation of sepals imbricate, margin of slipper-shaped labellum simple and straight, lightly incurved or recurved.....*Paphiopedilum* Pfitz.

Paphiopedilum callosum (Rchb. f.) Pfitz. and its var. *Sanderae* Hort.—*Paphiopedilum callosum* was described as *Cypripedium callosum* by H. G. Reichenbach filius (1896). It was brought from Siam by Alexandre Regnier, of Paris, in 1885, and very little time elapsed between its importation and the possession of a plant by the Sander's Company of St. Albans in England. It was early recognized as a graceful and vigorous form and was soon in culture wherever there were orchid enthusiasts. (See pl. 31.)

The albino form, variety *Sanderae*, appeared in culture in 1893 or 1894. Whether it flowered for the first time in England or France is a matter of debate; an anonymous article in the 'Journal of Horticulture' of 1912 says that it flowered for the first time in the autumn of 1893 in the collection of R. H. Measures, Esquire, at The Woodlands, Streatham. Be that as it may, in the Seventh Annual Show of the Royal Horticultural Society at the Inner Temple Gardens of May 23–25, 1894, it won a First Class Certificate when exhibited by Messrs. Sander and Sons of St. Albans. Both the Sander's plant and that of Measures appear to have come from the same source.

For several years the variety *Sanderae* remained something of a rarity but came at length to be well represented in collections everywhere; its similarity to the

albino form of *Lawrenceanum* was commented upon but it was considered by most to be more graceful.

Paphiopedilum Lawrenceanum (Rchb. f.) Pfitz. and its var. *Hyeanum* (Rchb. f.)—*Paphiopedilum Lawrenceanum* (see pl. 31) was described as *Cypripedium Lawrenceanum* by H. G. Reichenbach filius in 1878. The plant was found on the bank of the Lawas River by Mr. F. W. Burbidge while on a collecting trip in North Borneo in the service of the Veitch Company. In December, 1878, it was brought to flower in the Veitch greenhouses. Dr. Reichenbach named it for Sir Trevor Lawrence, Baronet, M. P., a contemporary orchid enthusiast whose collection is described as "being of exceptional richness and beauty" (Reichenbach, 1878).

The albino form appeared spontaneously in the Linden cultures of ordinary *Lawrenceanum* which had been imported by Messrs. Lowe & Co. of Clapton. Mr. Jules Hye of Ghent, a fancier, was most eager to secure such a rarity for his own collection, and apparently Mr. Linden, after having sold it to him, decided to name the plant for his customer. It was shown in the April 27, 1886, meeting of the Royal Horticultural Society by two exhibitors, the Compagnie Continetal, and R. B. White, Esquire, of Earlsfield, Surrey.

The new form was at first called *Cypripedium Hyeanum,* by various authors, but it was Reichenbach who first regarded it as a variety.[1] His description appeared in 'Lindenia,' of 1885, changing the nomenclature from *Cypripedium Hyeanum* (L.) Lind. & Rod. to *Cypripedium Lawrenceanum* Rchb. f. var. *Hyeanum* Rchb. f.

× *Paphiopedilum Maudiae* Hort.—The hybrid is a cross between *P. callosum* var. *Sanderae* and *P. Lawrenceanum* var. *Hyeanum,* with the latter as the seed parent (Wilson, 1923). It flowered for the first time in the early fall of 1900 in the houses of Messrs. Charlesworth & Co. of Heaton, Bradford, England, and on September 27 of that year took a First Class Certificate at the Manchester Orchid Society exhibition. A similar award was given when it was shown by Mr. G. W. Law-Schofield at the Royal Horticultural Society on July 30, 1901. Since that time it has been highly prized as a show plant, decorative plant, and commercial orchid. (See pl. 31).

Just who is to be credited with making the cross is a matter of conjecture. It has been reported that it was made in the Charlesworth establishment and again as having been made by two amateur growers, Major Mason and Mr. Charles Winn. In any event, the pot containing the seeds came into the possession of the Charles-

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[1] Reichenbach (Gard. Chron. 18:748) states: "Mr. Jules Hye Leysen, of Gand, Coupure 8, was so very kind as to send me the only flower we Europeans have had the opportunity of seeing . . . . I immediately thought it might be an albino of Sir Trevor Lawrence's *Cypripedium* . . . . I am persuaded we must regard it as *Cypripedium Lawrenceanum* variety *Hyeanum,* the name having been given, otherwise we might better call it 'Mons. Hye Leysen's individual' . . . . The history is simply, that it was found at the old establishment at Linden amidst a mass of typical *C. Lawrenceanum.*"

worth Company which is recorded as having produced the first flower. The plant was named for the daughter of Mr. Baguley, the Charlesworth foreman. The cross, of course, was inevitable since the parent forms were collector's items valued at more than 100 guineas a plant, a price which indicated the value then placed on such desirable forms.

There is a peculiarity in the nomenclature of the hybrid *Maudiae* which should be mentioned. If the specific, rather than the varietal, forms of the parent species had been crossed, the name *Maudiae* would have denoted a colored form. The albino form would then have to be designated by some such additional term as *albescens*. As it happened, × *Paphiopedilum Maudiae* denotes the albino form, and the colored hybrid which appeared six years later had to be designated *P. Maudiae* var. *coloratum*.

From the albino form, several selections have been made. Among them are *P. Maudiae* var. *magnificum*, *P. Maudiae* WESTONBIRT variety, *P. Maudiae* DELL variety, and *P. Maudiae* BANK HOUSE variety.

The interspecific hybrid *Paphiopedilum Maudiae* exhibits hybrid vigor in both growth and flowering, for it is sturdier than either of its parents and flowers more frequently. There are certain striking characters in the hybrid which are readily seen in one parent or the other. The following table compares some of these characters in parents and offspring:

	P. Lawrenceanum	*P. callosum*	× *Maudiae*
Leaves	Tessellated	Marbled	Tessellated
Petals	(a) Horizontal	Pendent or drooping	Intermediate (if otherwise it is closer to *callosum*)
	(b) Tip acute	Acuminate	Acute
	(c) Warted on upper and lower edges	Warted on upper edge only	Warted on upper edge only
Sepals	(a) Warted at base	Not warted at base	Not warted at base
	(b) Somewhat ciliate	Less ciliate	As in *callosum*

In order to clarify the positions of the species within the genus and the appearances of the entities involved, the following outline is added. The system is that of Pfitzer which is at present accepted but the only varieties mentioned are those bearing on this problem. All but the descriptions of *Maudiae* are from Sander's Orchid Guide of 1927.

Genus *Paphiopedilum*
Subgenus: OTOPEDILUM. (There are 3 subgenera. The others are BRACHYPETALUM and ANATOPEDILUM)
Section: PHACOPETALUM. (There are 11 sections of subgenus OTOPEDILUM)
Species:
1. *P. Curtisii*
2. *P. ciliolare*
3. *P. superbiens*
4. *P. Argus*
5. *P. barbatum*
6. *P. callosum*
   P. callosum var. *Sanderae*
7. *P. Lawrenceanum*
   P. Lawrenceanum var. *Hyeanum*

P. callosum: Foliage marbled. Scape 1 to 2 feet, 1- or 2-flowered. Flowers large, variable, dorsal sepal white, shaded or green at base, striped and often flushed with dark crimson, petals pale green with rose-purple apices, warted and ciliated at upper margins, lip brown-purple. Winter to summer.

Var. *Sanderae:* Dorsal sepal white with apple-green stripes and radiating dorsal veins, petals pale green, whitish on the upper edges, lip pale green. Winter to summer.

P. Lawrenceanum: Foliage brightly tessellated. Scapes 1–2 feet high. Flowers large, bold, dorsal sepal white with purple-red stripes, greenish at base, petals horizontal, greenish with purple shading, chiefly at the tips and margins, black-warted on both edges. Lip dull purple tinted with brown, variable. Summer.

Var. *Hyeanum:* Dorsal sepal pure white with green stripes, petals yellowish green, lip greenish. Summer.

× *P. Maudiae* (Rolfe, 1900): An albino. Dorsal sepal very broad and rounded, white closely veined with bright green. Petals somewhat falcate, light green with darker veins and a few darker warts on the upper margins. Lip and scape light green. Flowering time various.

II. STATUS OF *Paphiopedilum Maudiae* AS A PARENT PLANT

The hybrid *P. Maudiae* combines the winter-flowering habit of one parent with the summer-flowering habit of the other and is one of a small group of albinos within its genus. It is, furthermore, an exceptionally beautiful plant. These features would seem to make it a highly desirable parent yet it has not been used to great extent perhaps because of its sterility. When *Maudiae* has been used in what would appear to be advantageous crosses there has been little seed produced and the extended flowering period characteristic of *Maudiae* has, as a rule, not been obtained in the offspring.

Albino-flowered forms are rare in *Paphiopedilum,* the great majority of species as yet not having produced any. Although there is a considerable number of advanced[1] albino hybrids today, they may be traced back to one or more of these basic forms (Black, 1933; Cooper, 1946).

1. *P. bellatulum* var. *album* and *P. niveum* (subgenus BRACHYPETALUM). These are the only species in which true whites are formed. Even so *P. niveum* shows a faint peppering of purple when viewed closely.

2. *P. Lawrenceanum* (var. *Hyeanum*), *P. callosum* (var. *Sanderae*), and *P. Curtissii* (all in sect. PHACOPETALUM) have albino forms in which the white is striped and shaded with green. These belong to the "mottled group" characterized by marbled or tessellated foliage and petals ciliated and warted.

3. *P. Charlesworthii* var. *album* (sect. NEUROPETALUM) which may no longer be in cultivation.

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[1] In this study the expression primary hybrid is construed to mean species or variety hybrid. An advanced hybrid is one in which one or both parents is of hybrid origin.

4. *P. insigne* vars. *Sanderae* and *Sanderianum* (sect. NEUROPETALUM) is a soft yellow of variable depth according to the form. It is not striped, and white appears in the dorsal sepal. It is the chief member of the "insigne group."

Some success has been achieved by combining *Maudiae* with other albino varieties (Wilson, 1923):

HOLDENII *(Maudiae* × *callosum* var. *Sanderae)*.—Exhibited in 1909.

ALMA GAVAERT *(Maudiae* × *Lawrenceanum* var. *Hyeanum)*.—Flowered in 1911.

WARDEN *(Maudiae* × *Holdenii)*.—Flowered 1920.

EMERALD *(Maudiae* × *Curtissii* var. *Sanderae)*.—Exhibited in 1920.

ENCHANTRESS *(*ALMA GAVAERT × *Curtissii* var. *Sanderae)*.—Exhibited in 1921.

ROSETTII *(Maudiae* × *insigne* var. *Sanderianum)*.—Exhibited in 1908.

Before entering into a discussion of the crosses in which *P. Maudiae* and its parents have been involved, a further breakdown of the genus is necessary. The key given is taken from Pfitzer and may be used in conjunction with Charts I, II and III and their appendices:

KEY TO THE SUBGENERA OF *PAPHIOPEDILUM*

A. Labellum a slipper, exauriculate (without ears or auricles), bag-shaped, having a very short claw at the fore of the narrow inwardly rolled margin; petals very broadly elliptical or almost orbicular; leaves shortly elliptical, tessellated above, more or less purple below, scape uni- or bifloral .....Subgenus 1. BRACHYPETALUM Hallier[1]

B. Labellum a slipper, exauriculate, inclining downward, having a claw of almost equal length to that of the slipper on the front of the simple non-involute margin; petals elongate; leaves strap-shaped, green on both sides, scape several-flowered.....Subgenus 2. ANATOPEDILUM Pfitz.

C. Labellum a slipper, auriculate, bag-shaped, having a claw almost as long as the slipper at the fore of the simple, non-involute margin; petals elongate; leaves varying, scape several or single-flowered.....Subgenus 3. OTOPEDILUM Pfitz.

KEY TO THE SECTIONS OF THE SUBGENUS ANATOPEDILUM

A. Sepals striate between simple curving nerves; petals deflexed (bent outwardly), elongate with ciliate margins; staminode cylindrical, bent, the lower ascending part with long hair, the upper descending part glabrous above with two lobed apex.....Sect. GONATOPEDILUM Pfitz.

B. Sepals striate between simple curving nerves; petals deflexed, elongate, twisted margins adorned with hairy warts; staminode directed upward and forward, arched over, pilose below the concave margin.....Sect. CORYOPEDILUM Pfitz.

C. Sepals with extra striate curving nerves between tenuous reticulate nerves; petals curved, elongate, margin almost naked; staminode like that of the preceding section. .....Sect. PRENIPEDILUM Pfitz.

KEY TO THE SECTIONS OF THE SUBGENUS OTOPEDILUM

A. Staminode inversely heart-shaped, forked, enlarged on the back by a basal boss, acute, pilose. Leaves strap-shaped, uniform in tint, almost erect, green. Scapes several-flowered, flowering simultaneously.

a. Petals narrow, hanging, often twisted on the lower margin, decorated with hairy warts, minutely spatulate at the apex. Leaves very narrow with hyaline margins..... .....Sect. MYSTROPETALUM Pfitz.

b. Petals narrow from linear base toward the apex, frequently expanding into a blade, extremely divergent, nearly twisted, margin without warts. Leaves very narrowly yellow-margined .....Sect. PARDALOPETALUM Hallier

[1] *Brachypetalum* is not further divided to sections but is divided directly into species.

B. Staminode lightly forked, almost with an undivided boss at the back. Leaves broadly strap-shaped, recurved, uniform in tint, green or glaucous. Scape several-flowered, bracts emarginate, flowering successively.....Sect. COCHLOPETALUM Hallier
C. Staminode nearly orbicular, square, heart-shaped or almost heart-shaped. Sepals with tenuous reticulate nerves between simple curved nerves. Leaves green, uniform in tint, scapes unifloral, very rarely bifloral.
a. Staminode nearly square, enlarged on the back by 3 low, slightly prominent bosses; petals spatulate.....Sect. STICTOPETALUM Hallier
b. Staminode almost reverse heart-shaped, blunt, enlarged on the convex or plane back by one large central boss; petals more or less expanding into a blade toward the apex.....Sect. NEUROPETALUM Hallier
c. Staminode heart-shaped, furrowed at the back, slightly bossed; petals elliptical. .....Sect. THIOPETALUM Hallier
d. Staminode almost round, split on the posterior with rolled-back lobes; petals oblong with wavy margins.....Sect. CYMATOPETALUM Hallier
D. Staminode half-moon-shaped, the fore part equally three-cusped; sepals with simple curving nerves uniting reticularly at the apex; petals strongly sigmoid, bent outwards at the apex, erect. Leaves green, uniform in tint, scape unifloral..... .....Sect. CERATOPETALUM Hallier
E. Staminode half-moon-shaped, with double horse-shoe-shaped or now and then nearly rhombic boss. Sepals net-veined or simply veined, petals clearly expanding into a blade toward the apex. Leaves more or less tessellate (checkered), scape unifloral.....Sect. SPATHOPETALUM Pfitz.
F. Staminode moon-shaped or semi-rounded, without a boss; sepals simply nerved; petals not expanding or hardly expanding into a blade toward the apex. Leaves clearly tessellate, scape unifloral, rarely bifloral.
a. Petal margins naked or haired with equally disposed cilia..... .....Sect. BLEPHAROPETALUM Pfitz.
b. Petal margins spotted or adorned with prominent warts provided with small brush-like hair tufts.....Sect. PHACOPETALUM Pfitz.

Maudiae has been crossed to members of nine of the eleven sections of the subgenus OTOPEDILUM or to individuals whose antecedents lie within these sections. (It has not been crossed to individuals belonging to sections PARDALOPETALUM or MYSTROPETALUM.) The section contributing the most germ plasm to individuals crossed with *Maudiae* appears to be NEUROPETALUM; PHACOPETALUM, the section from which *Maudiae* stems, and CYMATOPETALUM contribute somewhat less. Individuals emanating from the NEUROPETALUM group were used freely, probably in efforts to combine *Maudiae's* everblooming character with some of the desirable "*insigne*" characters. Only one cross has been recorded with a BRACHYPETALUM species *(niveum)* and one with ANATOPEDILUM *(Rothschildianum* in sect. GONATOPEDILUM*)*. Of the 35 crosses in which *Maudiae* has been used (Sander's List, 1946), 11 have been with species, 3 with primary hybrids, and 21 with advanced hybrids. (See Chart I).

Paphiopedilum callosum has been crossed to members of nine out of the eleven sections of the subgenus OTOPEDILUM, or individuals having their antecedents therein. (It has not been crossed to individuals with a background in MYSTROPETALUM or PARDALOPETALUM). PHACOPETALUM, to which *callosum* and *Lawrenceanum* belong, is the section contributing the greatest number of individuals to these crosses with NEUROPETALUM and others contributing lesser numbers. It has been crossed to all of the species within the subgenus BRACHYPETALUM and with sections CORYOPEDILUM and PRENIPEDILUM of the subgenus ANATOPEDILUM.

Of its 55 crosses, 29 have been with species, 13 with primary hybrids, and 13 with advanced hybrids. (See Chart II and Appendix).

Paphiopedilum Lawrenceanum has been crossed to representatives of all of the eleven sections of Otopedilum. Again, Phacopetalum and Neuropetalum contribute the most germ plasm to the individuals used in these crosses, with other sections contributing lesser amounts. It has been crossed with all the Brachypetalum species and with individuals belonging to two of the sections of the subgenus Anatopedilum *(Gonatopedilum* and *Coryopedilum)*. Of the 62 crosses in which *Lawrenceanum* has been involved, 30 have been with species, 17 with primary hybrids, 15 with advanced hybrids. (See Chart III and Appendix).

The only reasonably complete list of orchid hybrids available is Sander's 'Complete List of Orchid Hybrids' (1946). This lists *Maudiae* as having been used in 35 crosses, *Lawrenceanum* in 62, and *callosum* in 55. Of the 35 offspring of *Maudiae* only 7 have been used to produce 41 named offspring of their own. Twenty *Lawrenceanum* offspring have been used in 123 crosses, and 15 *callosum* offspring in 74, with *Maudiae* being the most productive offspring in either case. It must be remembered, however, that Sander's List does not necessarily present a true picture of sterility or fertility. It simply lists the crosses giving rise to named and registered varieties and gives no account whatever of the crosses made wherein the grower considered the result not worth saving. It is thought, however, that most of the early crosses were named and registered since even the poor ones were regarded as having botanical interest.

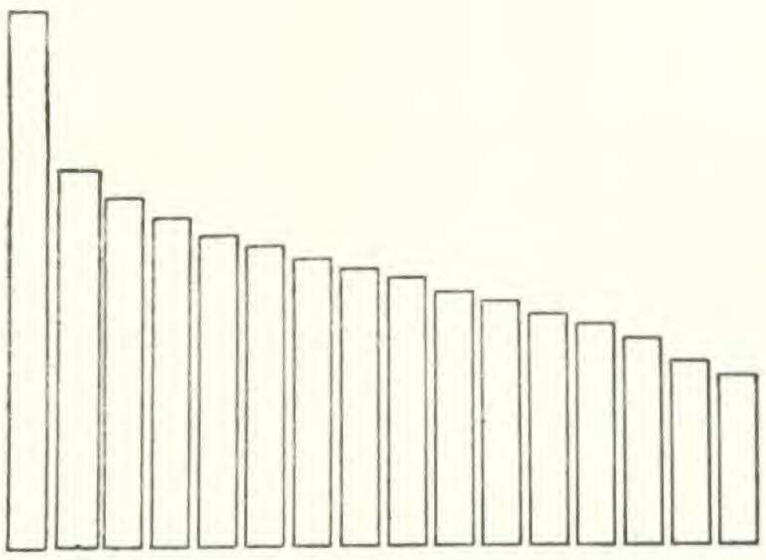
That both *Lawrenceanum* and *callosum* were crossed to more species than *Maudiae* is to be expected since they are older and have been known to horticulturists for a much longer time. It is reasonable to assume from the record that both of these species cross freely with other members of the genus. *Maudiae* appears to be slightly restricted, in comparison to its parents, in the number of sections to which it has been crossed. In part, this restriction may simply be a reflection of the horticulturist's discrimination; crosses made with *callosum* and *Lawrenceanum* that had proved inferior were probably not repeated with *Maudiae*. Also it is to be noted that many of the individuals to which *Maudiae* has been crossed have been advanced hybrids, and this has probably contributed to a lack of seed set. At any rate, hybridizers have not been able to obtain sufficient seed when using *Maudiae* as a parent to combine its undoubted qualities with those of other parents; large numbers of crosses must be made to obtain a small amount of seed.

III. Analysis of Root-Tips

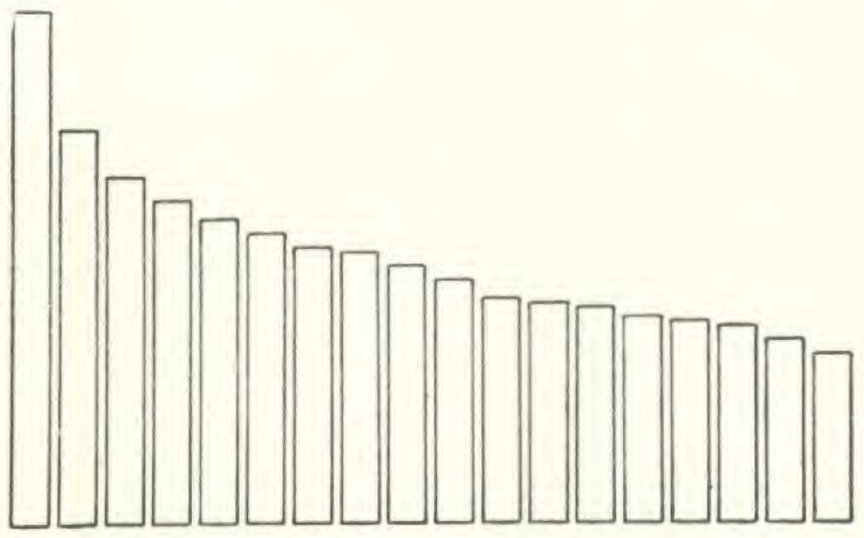
An attempt was made to analyze the chromosome complements of *P. callosum*, *P. Lawrenceanum* (the albino forms were not available), and several forms of × *Maudiae*. For this purpose root-tip smears were used. It was felt that in addition to observation with the microscope and scrutiny of camera-lucida drawings the construction of ideograms would be fruitful. The value of ideograms in this case will be discussed in a following paragraph.

Root-tips were killed and fixed, after quartering, in a solution containing six parts of absolute alcohol to three parts of chloroform to one part of glacial acetic acid. It was necessary to leave the tips in the killing and fixing fluid for at least fifteen minutes although they were often, for reasons of necessity, allowed to remain at least an hour. Tips that could not be squashed and stained immediately after removal from the killing and fixing fluid were kept in an aqueous solution of 45 per cent glacial acetic acid.

The first smears were made from tips of *P. callosum*. Aceto-orcein as well as aceto-lacmoid was used as a stain. After completing observations on *P. callosum* aceto-lacmoid only was used in studying *P. Lawrenceanum* and *P. Maudiae*. The squash procedure used was that outlined by Mehlquist (1947). It was found later in the investigation that the Feulgen technique outlined by Meyer (1943) gave excellent results generally but that for studies involving the centromere region aceto-lacmoid was the best agent when used on root tips that had not been in the Carnoy's fluid for more than fifteen minutes.



Text-fig. 1. *P. callosum*. Comparative length of chromosomes.



Text-fig. 2. *P. Lawrenceanum*. Comparative length of chromosomes.

The construction of ideograms was based upon camera-lucida drawings of mid-metaphase cells so flattened that all parts of a chromosome were in one plane. Ten such plates were obtained for *P. callosum* but only four could be found for *Lawrenceanum* and five for × *Maudiae*. It was the original plan to study ten of each, but, although many root-tips were examined, only this small number was found fit for use. Indeed, it was often difficult to obtain tips showing any divisions at all. On the basis of such small numbers the ideograms are presented here only as indicators and not as final pictures of chromosome complements. Haploid ideograms of *P. callosum* and *P. Lawrenceanum* based upon excellently flattened anaphase cells clearly indicating centromere position are presented. These were not used in the preparation of the final ideograms showing length relationships.

After preparation of camera-lucida drawings, the chromosomes were paired according to length, position of centromere, and placement of secondary constrictions. The basic ideogram thus consisted of the diploid number. For the final ideogram the lengths of the two members of a pair were averaged and the averages of all corresponding pairs were in turn averaged. The final ideogram therefore

shows the haploid number. The haploid ideograms of *P. callosum* and *P. Lawrenceanum* are fundamentally alike. Both show a noticeably long chromosome number 1. The difference in length between chromosomes 1 and 2 is less in *P. Lawrenceanum* than in the other. Aside from chromosome 1 all chromosomes show a very close intergradation in size. (See text-figs. 1 and 2.)

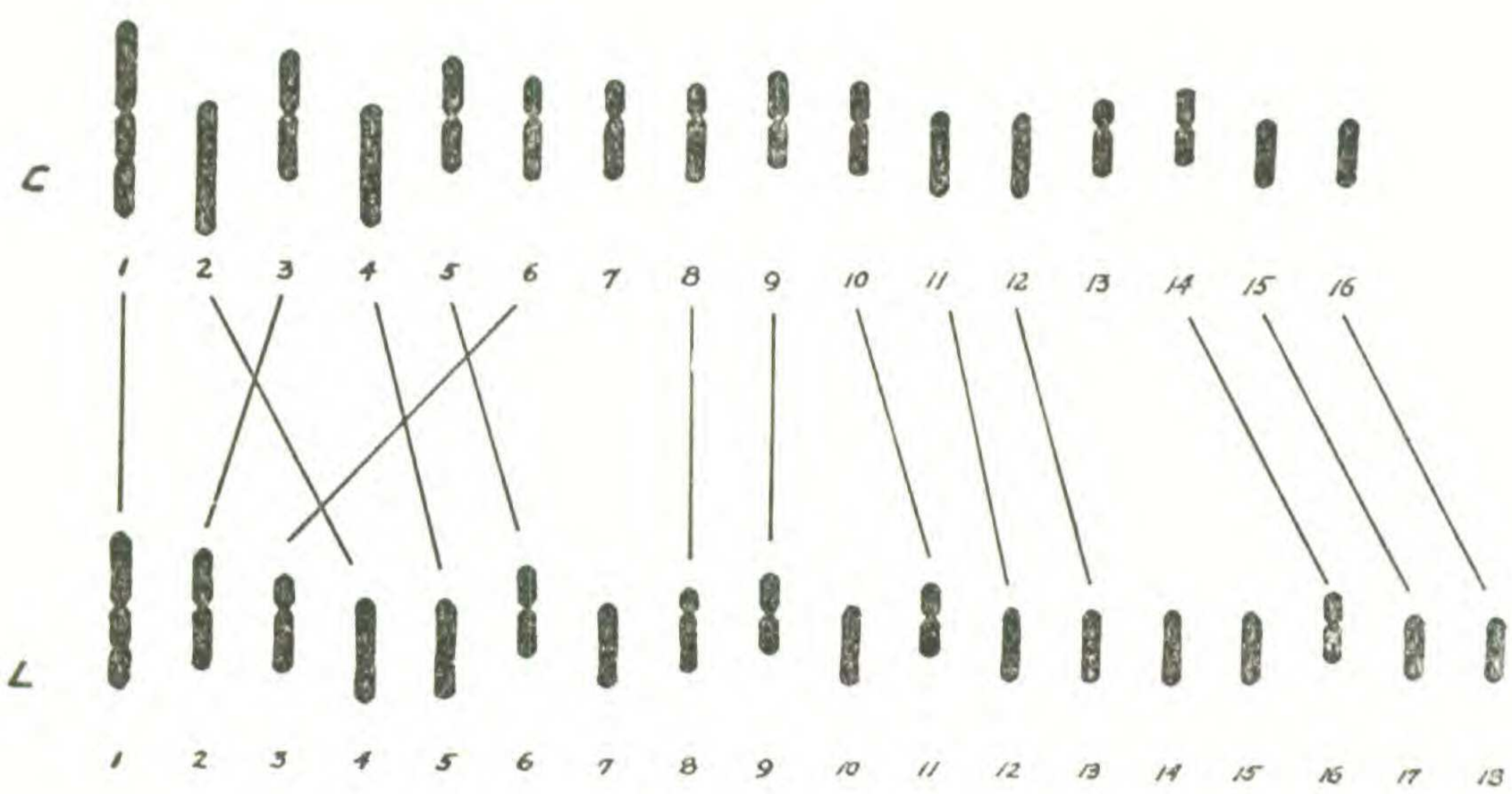
Chromosome counts in various "horticultural Cypripediums," including *P. callosum*, *P. Lawrenceanum*, and the interspecific hybrid *Maudiae*, have been made by Mehlquist (1947a), Duncan (1945, 1947), and others. Some of these counts were verified during this investigation: *P. callosum* has a diploid number of 32; *P. Lawrenceanum*, 36; × *Maudiae*, 34 (see pl. 32); *P. barbatum*, 38; *P. Curtissii*, 36; and *P. superbiens*, 38.

Paphiopedilum callosum, with a 2n number of 32, was analyzed first and ideograms were prepared. All but a few of the sixteen pairs of chromosomes have no identifying morphological features and exhibit a subtle intergradation in lengths. The following chromosomes are best recognized at sight:

1. The longest pair has median centromeres; the secondary constriction is about midway on one arm.

2. A pair intermediate in length often appears to be composed of three pieces of chromatin to each individual. An end piece is a satellite.

3. One pair, longer than average, each with one ball type end, appears to have subterminal centromeres.



Text-fig. 3. Diagrammatic representation of the chromosomes of *P. Lawrenceanum* (L) and *P. callosum* (c), based on anaphases in root-tips which clearly disclosed the position of the centromeres. Chromosomes arranged according to length. The numbers are merely for convenience and do not signify that chromosomes having the same numbers are alike. The lines connecting *c* and *L* chromosomes suggest possible homologues.

The second secondary constriction is on a chromosome of intermediate length with subterminal centromere in one species and on a chromosome with interstitial centromere in the other. The constriction is not shown because the positions of these chromosomes are uncertain.

4. One, or possibly two, pairs shorter than the average, with one ball type end, appears to have subterminal centromeres.

The remaining chromosomes are so alike morphologically and vary so little in length that they cannot be identified as individuals upon observation. However, it can be shown that within the *callosum* complement there are six terminal or subterminal pairs and ten pairs in which the centromeres are interstitial. (See text-fig. 3.)

The chromosomes of *P. Lawrenceanum*, by virtue of their similarity, remain as cryptic as those of *P. callosum*. Here the longest pair is readily identified by having a median, or close to median, centromere and is seen to possess a secondary constriction. Even the smallest chromosomes of *Lawrenceanum* cannot be distinguished readily because of their great similarity in length to the next smallest pair. Thus, aside from the longest pair, the remaining seventeen pairs verge closely on one another in size. The difference in the chromosome numbers of *P. callosum* and *P. Lawrenceanum* appears to be in an increase of small chromosomes in the complement of *P. Lawrenceanum*. It can be shown that in *P. Lawrenceanum* there are ten pairs of terminal or subterminal chromosomes and eight pairs in which the centromeres are interstitial. (See text-fig. 3.)

The chromosomes of the interspecific hybrid *Maudiae* presented the same morphological anonymity as those of the parental forms. Again the long pair with median centromere and clearly defined secondary constriction was readily noted. There are two pairs longer than the average with centromeres between the median and subterminal points, and two pairs of average length with median centromeres but these are not often readily discernible.

The satellited pair of intermediate length seen in *callosum* was seen in *Maudiae* and presented an interesting situation. In regard to this chromosome, *Maudiae* var. *magnificum* is visibly an inversion heterozygote. A cell was found in which it was apparent that half of one of the chromosomes of this pair is inverted. The inverted half bears the centromere, and since the centromere is subterminal in one, it becomes interstitial in the other.

The 2n chromosome configuration of *Maudiae* should consist of 10 chromosomes with terminal or subterminal centromeres and 8 with interstitial centromeres from the *Lawrenceanum* parent, while of the 16 chromosomes contributed by *callosum* 6 should be terminal or subterminal and 10 would be interstitial. Attempts to construct an ideogram showing the diploid number were not rewarding. It may be assumed from these attempts, however, that the close intergradation of chromosome lengths which characterize the parents is characteristic of the offspring.

The value of the ideograms in the analysis of these chromosome complements would appear to be at best only moderate. Ideograms can be used only as approximations for various reasons:

1. The lengths of members of a chromosome pair are not always equal; the longest chromosomes in the basic ideograms, for example, rarely agree exactly in

length. This may be a result of a squashing which leads to distortion not only in length but in other dimensions.

2. Lengths of chromosomes vary from metaphase to metaphase.

3. The length ratio of one pair to another may vary from one metaphase to another because of pressure applied in squashing.

4. The order of 16, 17 or 18 pairs in an ideogram must undoubtedly differ to some degree when there are many of approximately the same lengths lacking distinct morphological features and have been, in addition, subjected to pressure.

5. Centromeres may vary in size or become so small as to be apparently lacking.

6. Satellites vary in size as do also the portions of a multi-piece chromosome.

7. A chromosome may break under pressure not only at the centromere but at other regions. Thus a chromosome could appear to have a median centromere when it is actually of the subterminal type, or a median type, when broken in two, appear to be two subterminal chromosomes.

Despite these reasons for not placing too much faith in the ideogram as an actual picture of the chromosome complement there was sufficient resemblance among the basic ideograms to predict with considerable accuracy the appearance of the final ideogram.

Ideograms of the haploid numbers of various *Paphiopedilum* species published to date by Duncan and MacLeod (1948a, 1948b) include representatives of subgenera BRACHYPETALUM and ANATOPEDILUM and of the sections of OTOPEDILUM except SPATHOPETALUM, BLEPHAROPETALUM and PHACOPETALUM. These, for the most part, indicate a chromosome number 1 recognizable by its length and possessing a median or near median centromere. Chromosome number 2 may approximate or nearly approximate it in length but there is usually a difference. From chromosome number 2 on there is a close intergradation in length down to the smallest chromosome. In this they agree with ideograms published earlier by Francini (1931, 1932, 1934). Among the intermediate chromosomes there is one with a secondary constriction. These same generalities are true for the chromosomes of *P. callosum*, *P. Lawrenceanum*, and *P. Maudiae*, except that these three appear to have an additional secondary constriction on chromosome number 1. Only one species, *P. exul*, ideogrammed by Duncan and MacLeod, shows a secondary constriction on number 1 and none on any other chromosome. (Two species ideogrammed by Duncan and MacLeod exhibit a secondary constriction on number 2 and on no other chromosomes. These are *P. Druryi* and *P. Spicerianum*.)

The following list presents the 2n chromosome numbers to date of species within the genus:

CHROMOSOME NUMBERS OF SPECIES OF PAPHIOPEDILUM

	Chromosome Numbers	Authority*	Date
Subgenus BRACHYPETALUM Hallier			
P. bellatulum (Reichb. f.) Pfitz.	26	D	'47
	26	GM	'47
P. concolor (Batem.) Pfitz.	26	D&ML	'48
P. niveum (Reichb. f.) Pfitz.	26	GM	'47
	26	D	'47
P. Delanatii Guill.	26	D	'47
	26	GM	'47
Subgenus ANATOPEDILUM Pfitz.			
Sect. GONATOPEDILUM Pfitz.			
P. Rothschildianum (Reichb. f.) Pfitz.	26, 28	D	'47
	26	D&ML	'49
Sect. CORYOPEDILUM Pfitz.			
P. praestans (Reichb. f.) Pfitz.	28	D	'47
	28	D&ML	'49
P. philippinense (Reichb. f.) Pfitz.	26	D&ML	'49
Sect. PRENIPEDILUM Pfitz.			
P. Stonei (Hook. f.) Pfitz.	26	D	'47
MARY REGINAE Hort.	26	D&ML	'49
Subgenus OTOPEDILUM Pfitz.			
Sect. MYSTROPETALUM Pfitz.			
P. Parishii (Reichb. f.) Pfitz.	26	D	'47
	26	D&ML	'49
Sect. PARDALOPETALUM Hallier			
P. Lowii (Lindl.) Pfitz.	26	D	'47
	26	D&ML	'49
P. Haynaldianum (Reichb. f.) Pfitz.	26	D	'47
	26	D&ML	'49
Sect. COCHLOPETALUM Hallier			
P. Chamberlainianum (O'Brien) Pfitz.	26	D	'47
P. glaucophyllum J. J. Smith	36	D	'47
Sect. STICTOPETALUM Hallier			
P. hirsutissimum (Lindl.) Pfitz.	26	D&ML	'49
Sect. NEUROPETALUM Hallier			
P. villosum (Lindl.) Pfitz.	26	F	'34
	28	F	'31
	26	GM	'47
	26	D	'47
	26	D&ML	'48
P. Boxallii (Reichb. f.) Pfitz.	26	GM	'47
	26	D&ML	'48

* The abbreviations used for authorities are: D, Robert E. Duncan; D&ML, Robert E. Duncan and Raymond A. MacLeod; F, Eleanora Francini; GM, Gustav A. L. Mehlquist.

	Chromosome Numbers	Authority*	Date
P. insigne (Wall.) Pfitz.	32	F	'31
	26	GM	'47
	26	D	'47
	26	D&ML	'48
P. exul (O'Brien) Pfitz.	26	D	'47
	26	D&ML	'49
P. Charlesworthii (Rolfe) Pfitz.	26	D	'47
	26	D&ML	'49
P. Gratrixianum Rolfe	26	D	'47
	26	D&ML	'48
Sect. THIOPETALUM Hallier			
P. Druryi (Bedd.) Pfitz.	26	D	'47
	26	D&ML	'49
Sect. CYMATOPETALUM Hallier			
P. Spicerianum Pfitz.	30	F	'31
	28	D	'47
	28, 30	D&ML	'49
Sect. CERATOPETALUM Hallier			
P. Fairrieanum (Lindl.) Pfitz.	26	D	'47
	26	GM	'47
	26	D&ML	'49
Sect. SPATHOPETALUM Pfitz.			
P. venustum (Wall.) Pfitz.	36	F	'31
	42	D	'47
Sect. BLEPHAROPETALUM Pfitz.			
P. tonsum (Reichb. f.) Pfitz.	34	D	'47
P. Mastersianum (Reichb. f.) Pfitz.	32	D	'47
P. javanicum (Reinw.) Pfitz.	36	D	'47
P. Dayanum (Reichb. f.) Pfitz.	34	D	'47
P. Wardii Summerhayes	40-45	D	'45
Sect. PHACOPETALUM Pfitz.			
P. Curtisii (Reichb. f.) Pfitz.	36	D	'47
	36	GM	'47
P. superbiens (Reichb. f.) Pfitz.	38	D	'47
P. barbatum (Lindl.) Pfitz.	32	F	'31
	38	F	'34
	38	D	'47
	38	GM	'47
P. callosum (Reichb. f.) Pfitz.	32	D	'47
	32	GM	'47
P. Lawrenceanum (Reichb. f.) Pfitz.	36	D	'47
	36	GM	'47

IV. MEIOSIS

Aceto-lacmoid and aceto-orcein gave metaphase I smear preparations which were clear enough to determine the nature of pairing but the outlines of the chromosomes were often not sharply defined. A modification of the Feulgen technique, although somewhat better, gave much the same result. These methods also proved unsatisfactory for a study of the prophase chromosomes; all of these methods seemed reasonably good for material in anaphase I or later stages. The difficulty was not remedied even when an iron aceto-carmine mordant was added to the Carnoy's Fluid used for killing and fixing. The situation was further complicated by restrictions on the number of buds available; forty were used in the course of the study of pollen mother cells. It must be remembered that none of the plants involved are frequent bloomers, the parental forms blooming once yearly and *Maudiae* at most twice.

It was found after considerable experimentation that the best preparations were obtained by making permanent slides. Anthers were dropped in Carnoy's Fluid for 10–15 seconds and then put in CRAF for 24 to 48 hours. They were then washed and run through the usual tertiary butyl alcohol series and, after infiltration, were embedded. Sections were cut at 10 μ and then stained in crystal violet and safranin (Stockwell, 1934). This method gave results in pachytene and early diplotene which could not be obtained with the smear methods mentioned above, and the metaphase chromosomes were sharply outlined. A peculiarity in the staining effect was noted with the use of crystal violet and safranin. When the slides were left in the stain for a long time both meiotic and mitotic chromosomes were stained dark purple. When exposed to the stain for about 15 minutes the meiotic chromosomes were red while the mitotic nuclei or chromosomes were blue. At an exposure of about 12 minutes both meiotic and mitotic chromosomes were red.

No satisfactory study of chiasmata was made because of the extremely reduced size of the bivalents at mid-metaphase and because the procedure adopted does not spread the chromosomes sufficiently as the smear method so often does. Diakinesis, a stage favorable for the study of chiasmata in many other plants, could not be prepared suitably by any of the methods cited above.

P. Maudiae Hort. var. *magnificum* furnished most of the hybrid material studied although WESTONBIRT and DELL varieties were examined; the last do not appear to differ from *magnificum*.

PAPHIOPEDILUM CALLOSUM (2n = 32)

Prophase I.—Pairing appears to be normal when viewed in the pachytene stage. Permanent preparations of diakinesis in *callosum* resemble those of *Maudiae* prepared by aceto-lacmoid smears or the Feulgen technique. Within the various techniques employed in this study it may be said that diakinesis in the two species and the hybrid is not a favorable stage for study. The chromosomes appear to be in a fluid or somewhat fluid state and are therefore poorly defined by the stain; large patches of chromatin are occasionally seen where the chromosomes appear to

have stuck together. This perhaps represents a time when the matrix is being elaborated most freely and is therefore quite thin in consistency. Some chiasmata can be seen but no accurate over-all picture can be given. Occasionally they appear as relatively colorless strands between the ill-defined chromosomes and again they appear to be surrounded with enough matrix to render them stainable. Among the chromosomes of intermediate length, two ring configurations have been noticed: one with no free ends and another in which one of the chiasmata is apparently not terminalized so that a short portion of one end of each chromosome is free. The same pair may be involved in both cases. Among the shortest chromosomes (at least those with subterminal centromeres) bivalents are formed with only one chiasma. The longest pair appears to form three or four chiasmata. The nucleolus is plainly visible at diakinesis.

Metaphase I.—Metaphase chromosomes have not been stained as clearly as desired by smear methods but were clear enough to determine pairing; chiasmata could not be properly interpreted. Twenty-five metaphase cells examined showed pairing to be in 16 bivalents. (See pl. 32).

Of 114 metaphase plates seen in side view, 107 appeared to have all their chromosomes in the plate in the normal fashion. One cell appeared to have one lagging chromosome, 2 were doubtful as to fragments or isolated chromosomes, and 5 appeared to have isolated chromosomes or fragments in each. It is entirely possible that these apparent abnormalities existed as a result of smearing.

Anaphase I.—Fifty-six anaphase cells were examined and no anaphase bridges were observed. One cell appeared to have a fragment between the two poles. Anaphase appears to be normal.

Telophase I.—No cell wall is formed at the close of division I. An interphase nucleus is formed.

Telophase II.—Five hundred tetrads were examined. No micro-grains or small extra cells were found within the thick wall.

Pollen grains.—Pollen grains were mounted in aceto-lacmoid for staining but were not pressed. The grains are elliptical to spherical in shape. Of 500 grains examined only 8 were found to be empty; no shrunken or distorted grains were found. The grains are slightly smaller than those of *P. Maudiae.* (See section on pollen grains, × *Paphiopedilum Maudiae*).

PAPHIOPEDILUM LAWRENCEANUM (2n = 36)

Prophase I.—No leptotene or zygotene nuclei have been studied but pachytene and early diplotene nuclei have been observed. The crystal violet-safranin technique was used. Pairing as observed in pachytene appears to be regular throughout and no abnormalities were noticed. The early diplotene stages examined show the initial repulsion between the paired chromosomes.

Metaphase I.—Only 2 metaphase I cells suitable for study were found. These indicated pairing to be in 18 bivalents.

Anaphase I.—Observations on a large number of these cells indicate no apparent abnormalities. Bridges are not formed nor do there appear to be any lagging chromosomes or fragments in evidence. The chromosomes do not appear to be split in readiness for division 2 at this stage.

Telophase I.—An interphase nucleus is formed at this stage but no cell wall is formed. Eighteen chromosomes were counted at one pole in an early telophase.

Metaphase II.—Examination of metaphase II cells indicated that division had been regular. The regularity with which 18 chromosomes are disposed to each pole serves as additional evidence that 18 bivalents are formed at metaphase. (See pl. 32).

Anaphase and Telophase II.—No abnormalities are evident and the tetrads formed resemble those of *P. callosum*. A tetrad was found in which 18 chromosomes could be counted at one pole.

Pollen grains.—Pollen grains are elliptical to spherical and about the same size as the *callosum* grains. Of the 500 grains examined, only 2 were found to be empty. (See section on pollen grains, × *Paphiopedilum Maudiae.*)

× *PAPHIOPEDILUM MAUDIAE* Hort. (2n = 34)

Prophase I.—In the pachytene of *P. Maudiae* the nucleolus appears as a well-defined almost colorless body in intimate contact with chromosomal material. Although in sectioning the knife may frequently remove the nucleolus from cells, it is visible nonetheless in many others. Its attachment to a chromosome is noticeable. It is impossible to tell which chromosome is involved since the pachytene nucleus represents a tangle of long slim threads whose ends, except in chromosomes cut through by the knife, are often not visible. As with *callosum* and *Lawrenceanum* two nucleoli are occasionally visible in the mitotic cells forming the jacket around the pollen mother cells but only one nucleolus has been seen in the PMC's. The nucleoli seen in the PMC's are larger than those seen in mitotic cells.

There have been observed in the pachytene and pachytene-early diplotene chromosome configurations which suggest inversion and deletion but the chromosomes are so attenuate and the suspected loops or buckles so small that it has been impossible to ascertain this. The presence of inversion loops in pairing is to be expected in view of the presence of anaphase bridges.

As in *Lawrenceanum* the beadlike effect of the chromomeres is evident at this stage.

Metaphase I.—The staining with smear methods was suitable enough to examine pairing. Of the 27 metaphase cells of *P. Maudiae* examined, 26 showed 17 bivalent chromosomes. (See pl. 34). One cell showed 16 bivalents and 2 univalents. It appears that two of the *Lawrenceanum* chromosomes are pairing.

Anaphase I.—A total of 483 anaphase I cells were examined and several abnormalities were found:

a. Cells with 1 bridge but no fragments	17
b. Cells with 2 bridges but no fragments	1
c. Cells with 1 bridge and 1 fragment	13
d. Cells with 1 bridge and 2 fragments	1
e. Cells with 2 bridges and 1 fragment	2
f. Cells with 1 fragment (or small isolated chromosome)	15
TOTAL	49

Of the cells examined 10.1 per cent showed abnormalities.

A further analysis of anaphase I was made possible through the observation of 4 cells in which the chromosomes could be counted at one or both poles. While this number is far too small to be regarded as significant the information is included to amplify the notes above.

1. Two cells showed clearly 17 chromosomes at one pole but a count could not be made at the other pole. There were no lagging chromosomes in evidence. The chromosomes were split in readiness for division 2 but this partial separation may have been caused by smearing.

2. One cell showed 17 chromosomes at one pole and 16 at the other. One chromosome lagged but appeared to be slightly closer to the pole with 17. Again the chromosomes were split.

3. One cell had 17 chromosomes at each pole; these were split for division 2.

Tetrads.—Examination of 527 tetrads was made. The arrangement is primarily that of 2 cells in each of two planes although 4 in one plane is not rare. The presence of a micro-grain or micro-cell, a small, extra cell within the tetrad wall, was occasionally noted.

Apparently normal groups:	
1. Two cells in each of two planes	417
2. Four cells in one plane	72
Apparently abnormal groups:	
1. Two cells in two planes plus one micro-grain	28
2. Four cells in one plane plus one micro-grain	4
3. Two cells in one plane (diad) plus one micro-grain	1
4. Three cells in one plane (triad) plus one micro-grain	5
TOTAL	527

Of tetrads examined 7.2 per cent showed irregularities.

Pollen.—In general the pollen grains range from elliptical to spherical. Of 500 grains examined 54 (10.8 per cent) were empty and some of them were distorted. (See pl. 33). Four of the empty grains were about one-third the normal size. The full regular cells are slightly larger than those of *P. callosum* and *P. Lawrenceanum.*

Measurements of 100 *Maudiae* pollen grains and 100 each of *callosum* and *Lawrenceanum* indicated that those of *Maudiae* average .0580 mm. along the long axis, while those of *callosum* and *Lawrenceanum* are .0530 and .0526 respectively. That the slight difference in size between the grains of the offspring and the parents is not merely based on variation within the samples was confirmed with a standard deviation test.

In both species and in the hybrid, leptotene and zygotene probably occur when the bud is quite small. Just how soon pachytene begins is not known but apparently pachytene and pachytene-early diplotene go on for considerable time, sometimes even a matter of days, depending upon environmental conditions. The remaining stages, particularly diakinesis and metaphase I, progress rapidly.

The lengths of some buds, divested of enfolding bracts, are listed together with the meiotic stages exhibited:

P. callosum

13.0 mm.....Pachytene

15.0 mm.....Pachytene

16.5 mm.....Pachytene to diakinesis; Early metaphase I; Metaphase I

17.0 mm.....Primarily diads. A few metaphase and anaphase I cells

18.0 mm.....Tetrads

P. Lawrenceanum

16.5 mm.....Pachytene, early diplotene

18.0 mm.....A few metaphase and anaphase I cells but chiefly division 2; Division 2; Tetrads

18.5 mm.....Division 2

19.0 mm.....Pollen grains

× *P. Maudiae*

13.0 mm.....Pachytene

15.5 mm.....Pachytene

16.5 mm.....Diakinesis to early metaphase I

17.0 mm.....Pachytene; Pachytene to diakinesis; Pachytene to mid-metaphase I

18.0 mm.....1. Metaphase I
2. Telephase I through division 2

18.5 mm.....Tetrads

V. DISCUSSION

It will be noticed in the anaphase I data of the hybrid that of the 49 cells listed as showing disorders, group *c* (13 cells) is characterized by one bridge and one fragment. This is the typical result of pairing between two chromosomes when one of them has an inversion not involving the centromere and a crossover occurs within the inverted region.

Group *a* (17 cells) exhibits the bridge but no fragment. Two possibilities exist here: either the fragment was not visible or it did not exist. Since none of the fragments observed either with or without bridges were large it is possible that in these cases it had been displaced by smearing or that it had been concealed by

the chromosomes at one or the other of the poles. There being evidence that inversions exist, this possibility must be given the more credence. The other possibility is that in these cells no fragment existed as a result of an inversion bridge. This would necessitate another hypothesis for the origin of a bridge without a fragment, and there is no evidence here to support such a hypothesis. The single cell in group *b* with two bridges but no fragments should be considered in the same light except that in this group two chromosome pairs were probably involved.

Group *e* (2 cells) is characterized by two bridges and one fragment. The most logical assumption here is that one of the fragments was rendered invisible as in the case above. The single instance of one bridge and two fragments *(d)* may well indicate the breakage of one bridge before the other. In these cases, as in *b*, two chromosome pairs would be involved.

Group *f* is composed of 15 cells which showed one fragment or small isolated chromosome. It is thought that these were true fragments since they were quite small. In such a case the bridge would have been already broken. However, the possibility that these might have been lagging chromosomes cannot be overlooked since many of the typical mid-metaphase I bivalents of the hybrid are small.

An interesting case is presented by the pair of chromosomes of intermediate length with prominent secondary constriction. It is this pair which exhibits the inversion mentioned in the section on root-tip analysis. (See pl. 32). Half of the chromosome is involved in the inversion for which the hybrid examined is heterozygous, and the inversion, when viewed under the microscope, appears to be terminal. The possibility must not be overlooked that there is chromatin material here which cannot be seen and would render the inversion interstitial. It has long been felt that inversions generally did not involve chromosome ends (Darlington, 1937; Kossikov & Muller, 1935; Muller, 1938). However, there is considerable evidence to date that terminal inversions do occur (Kauffmann, 1937; Sutton, 1940; Carson, 1944; Carson & Stalker, 1947), and the possibility that the inversion mentioned here is truly terminal must not be brushed aside. This inversion, since it involves the centromere, would not bring about the formation of a bridge. A single crossover within the inversion would result in a duplication-deficiency chromatid as well as one complete chromatid going to each pole. Of the complete chromatids, one would show the inversion (Sturtevant & Beadle, 1939).

It will be noticed that although 10.1 per cent of the anaphase I cells exhibited disorders, only 7.2 per cent of the hybrid tetrads were visibly abnormal. This probably can be taken to mean that some of the tetrads, although appearing normal, are not so. It cannot be said that there is any absolute correlation between the 10.8 per cent visibly non-viable pollen and the similar percentage of visible anaphase I abnormalities even though it is suggestive. No doubt there are other factors to be considered. The 10.8 per cent of non-staining pollen grains is not a true estimate of the hybrid's sterility in view of growers' experiences in attempting to use *Maudiae* as a parent plant. There are, no doubt, many pollen grains which appear quite normal but whose viability is terminated at later stages. Male gametes

may become non-viable in the pollen tube; the pollen tube may grow too slowly; the egg may be non-viable; the zygote may be non-viable; or the seedling perish early in its existence.

That the 10.8 per cent non-viable pollen is not a complete picture of the sterility of the hybrid is supported by what is known of pairing in *Maudiae*. It will be remembered that pairing in *Maudiae* was typically indicated by 17 bivalents at metaphase I. This suggests pairing between two *Lawrenceanum* chromosomes, and if two chromosomes are like enough to pair consistently this would in turn suggest polyploidy. It is entirely reasonable to assume that such pairing is the result of polyploidy. A glance at the list of chromosome numbers at the close of section III reveals that throughout subgenera BRACHYPETALUM and ANATOPEDILUM the *n* number is 13. In the subgenus OTOPEDILUM, the group to which all of the individuals dealt with in this study belong, higher *n* numbers approach the triploid level. It is suggested that this increase in chromosome number is the result of hybridization between groups that cannot be named at this time for lack of evidence.

The mere statement that pairing in *Maudiae* is in 17 bivalents and that the 2 remaining *Lawrenceanum* chromosomes pair is probably an over-simplification. *P. callosum* is characterized, as we have seen, by a chromosome set of 6 pairs of terminal or subterminal chromosomes and 10 interstitial pairs while *P. Lawrenceanum* possesses 10 terminal or subterminal pairs and 8 interstitial pairs. The difficulties of pairing a *Lawrenceanum* and a *callosum* chromosome for each of 16 bivalents (in addition to the bivalent already formed by each of two *Lawrenceanum* chromosomes), in view of the differences in morphology, are apparent. It is highly probable that some *callosum* chromosomes are pairing amongst themselves as well as with *Lawrenceanum* chromosomes, and this possibility would exist equally well for chromosomes of *Lawrenceanum*. Under such conditions gametes could be produced which would lack necessary genic elements. From the foregoing facts it seems logical to conclude that the causes of sterility in the hybrid are:

1. Visible disorders in anaphase I due to inversions.
2. Invisible disorders at anaphase I due to an inversion which includes the centromere and therefore results in duplication-deficiencies.
3. Pairing of some *callosum* chromosomes and some of the *Lawrenceanum* chromosomes among themselves (because of their polyploid background) takes place so that some of the gametes are without necessary chromatin material.

VI. SUMMARY

1. A cytological study was made of the × *Paphiopedilum Maudiae* Hort., the result of a cross between the albino forms of *P. callosum* and *P. Lawrenceanum*. Because of its high sterility, *P. Maudiae* as a parent plant has rarely, if ever, produced any offspring of a quality equal to, or exceeding, its own.

2. A short discussion of the genus and the histories of the parental forms and the offspring are set forth.

3. Some observations are made on the status of × *Paphiopedilum Maudiae* Hort. as a parent plant.

4. A cytological analysis of root-tips of the parental forms and the hybrid gave the following results:

a. Chromosome numbers of *P. callosum*, *P. Lawrenceanum*, and *P. Maudiae* are confirmed as being 32, 36, and 34, respectively. Two other species counts were also confirmed (*P. barbatum*, 38; *P. Curtissii*, 36; *P. superbiens*, 38).

b. *P. callosum* has 6 pairs of chromosomes with terminal or subterminal centromeres and 10 pairs with interstitial centromeres.

c. *P. Lawrenceanum* has 8 pairs with interstitial centromeres and 10 with terminal or subterminal centromeres.

d. *P. Maudiae* is heterozygous for an inversion which seems to be terminal.

5. Study of meiosis in the parental forms and the hybrid gave the following results:

a. *P. callosum* and *P. Lawrenceanum* undergo normal meioses with bivalent pairing.

b. Pairing in *P. Maudiae* is in 17 bivalents. Some disorders are visible at anaphase I.

c. Only 10.8 per cent of the *Maudiae* pollen grains are visibly nonviable. This does not give a true picture of the sterility of the plant.

6. Some conclusions are offered as to the several causes of sterility of the hybrid:

a. Inversions that give rise to anaphase I disorders.

b. An inversion, visibly terminal upon microscopic examination, which does not give rise to visible anaphase I disorders because it includes the centromere.

c. As a result of polyploidy in the genus some of the *callosum* chromosomes pair with themselves as do some of the *Lawrenceanum* chromosomes in meiosis of hybrid pollen mother cells. Some of the gametes are therefore deprived of necessary chromatin material.

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CHART I

A LIST OF THE CROSSES IN WHICH P. MAUDIAE HAS BEEN USED AS A PARENT.

THE NUMBERS BELOW EACH VARIETAL NAME INDICATE HOW MANY TIMES THE VARIETY HAS BEEN USED AS A PARENT.
TO THE RIGHT OF THE ANTECEDENT SPECIES ARE THE SECTIONS OF OTOPEDILUM OR THE SUBGENERA TO WHICH THEY BELONG.

MAUDIAE (SECTION PHACOPETALUM OF SUBGENUS OTOPEDILUM)
35

1. X ACTAEUS = MAUD GREEN. ACTAEUS (84 / 0)
   - INSIGNE — NEUROPETALUM
   - LEEANUM
     - INSIGNE — NEUROPETALUM
     - SPICERIANUM — CYMATOPETALUM

2. X ALMA GAVAERT = ALMAUD. ALMA GAVAERT (11 / 0)
   - MAUDIAE
     - CALLOSUM VAR. SANDERAE — PHACOPETALUM
     - LAWRENCEANUM VAR. HYEANUM — PHACOPETALUM
   - LAWRENCEANUM VAR. HYEANUM — PHACOPETALUM

3. X ARMISTICE II = ARMAMENT. ARMISTICE II (12 / 0)
   - ANTINOUS
     - ACTAEUS
       - INSIGNE — NEUROPETALUM
       - LEEANUM
         - INSIGNE — NEUROPETALUM
         - SPICERIANUM — CYMATOPETALUM
     - J. HOWE – ?
   - NITENS
     - INSIGNE — NEUROPETALUM
     - VILLOSUM — NEUROPETALUM

4. X AUREUM = BENITA. AUREUM (58 / 0)
   - NITENS
     - INSIGNE — NEUROPETALUM
     - VILLOSUM — NEUROPETALUM
   - SPICERIANUM — CYMATOPETALUM

5. X BINGLEYENSE = COLOURFUL. BINGLEYENSE (21 / 0)
   - CHARLESWORTHII — NEUROPETALUM
   - HARRISIANUM
     - BARBATUM — PHACOPETALUM
     - VILLOSUM — NEUROPETALUM

6. X CALLOJO-BARBATUM = METEORITE. CALLOJO-BARBATUM (10 / 0)
   - CALLOSUM — PHACOPETALUM
   - BARBATUM — PHACOPETALUM

7. X CALLOSUM = HOLDENII. CALLOSUM (SP.) (55 / 6) — PHACOPETALUM

8. X CHAMBERLAINIANUM = IRIS II. CHAMBERLAINIANUM (SP.) (36 / 0) — COCHLOPETALUM

9. X CILIOLARE = COLORADO CILIOLARE (SP.) (27 / 0) — PHACOPETALUM

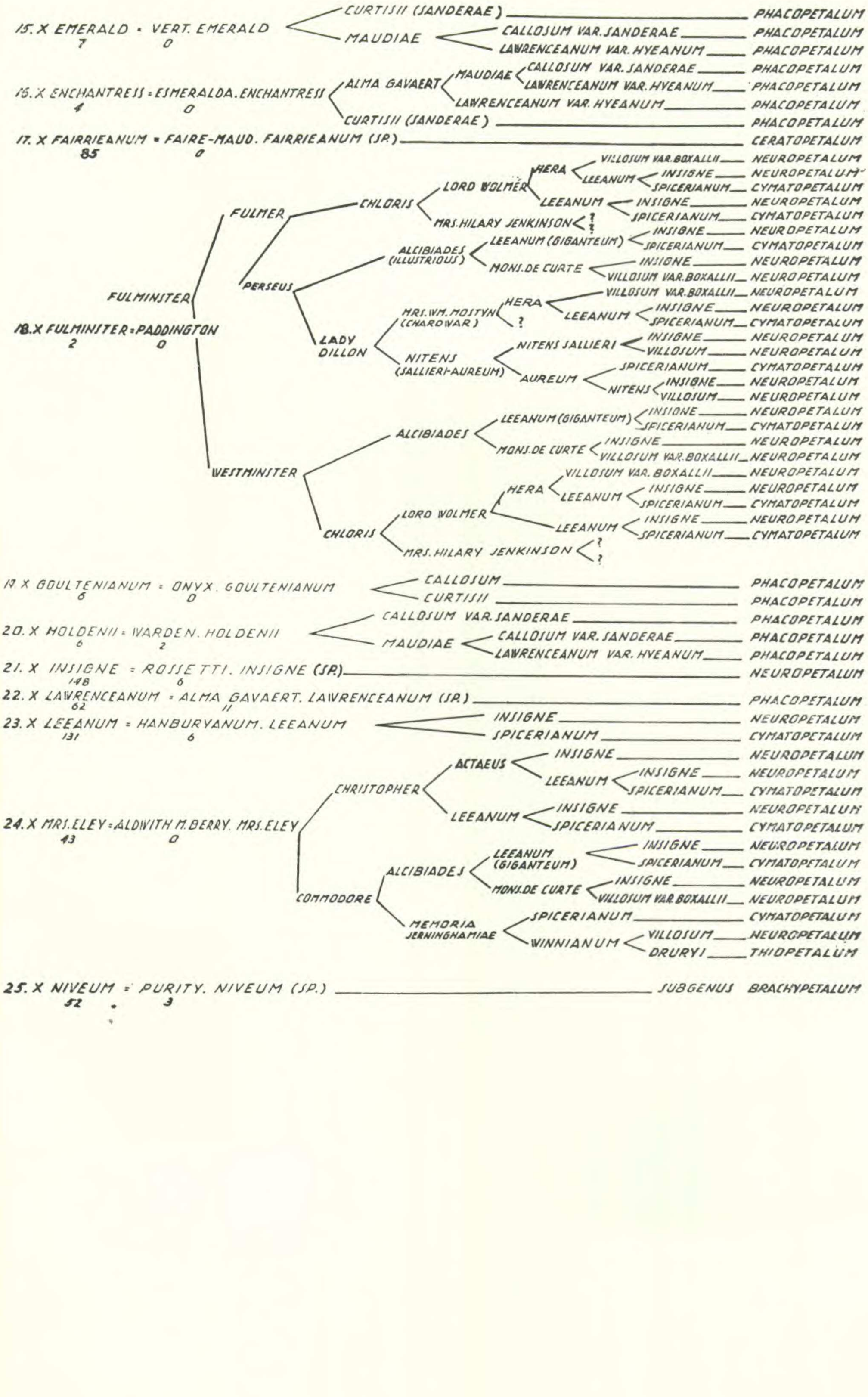
10. X CLAIRE DE LUNE = MITYLENE. CLAIRE DE LUNE (2 / 0)
    - EMERALD
      - CURTISII (SANDERAE) — PHACOPETALUM
      - MAUDIAE
        - CALLOSUM VAR. SANDERAE — PHACOPETALUM
        - LAWRENCEANUM VAR. HYEANUM — PHACOPETALUM
    - ALMA GAVAERT
      - MAUDIAE
        - CALLOSUM VAR. SANDERAE — PHACOPETALUM
        - LAWRENCEANUM VAR. HYEANUM — PHACOPETALUM
      - LAWRENCEANUM VAR. HYEANUM — PHACOPETALUM

11. X CRUSADER = PALESTINE. CRUSADER (8 / 0)
    - JULIAN
      - AUREUM (OEDIPPE)
        - NITENS JALLIERI HYEANUM
          - INSIGNE — NEUROPETALUM
          - VILLOSUM — NEUROPETALUM
        - SPICERIANUM MAGNIFICUM — CYMATOPETALUM
      - VAN DYCK
        - HIRSUTISSIMUM HYBRID — STICTOPETALUM
        - MONS. DE CURTE
          - INSIGNE — NEUROPETALUM
          - VILLOSUM VAR. BOXALLII — NEUROPETALUM
    - LUCIFER
      - HERA (EURYADES)
        - VILLOSUM VAR. BOXALLII — NEUROPETALUM
        - LEEANUM
          - INSIGNE — NEUROPETALUM
          - SPICERIANUM — CYMATOPETALUM
      - NIOBE
        - SPICERIANUM — CYMATOPETALUM
        - FAIRRIEANUM — CERATOPETALUM

12. X CURTISII = EMERALD. CURTISII (SP.) (44 / 7) — PHACOPETALUM

13. X DORA = MAUDORA. DORA (5 / 0)
    - ACTAEUS
      - INSIGNE — NEUROPETALUM
      - LEEANUM
        - INSIGNE — NEUROPETALUM
        - SPICERIANUM — CYMATOPETALUM
    - ILLUSTRE
      - LATHAMIANUM
        - SPICERIANUM — CYMATOPETALUM
        - VILLOSUM — NEUROPETALUM
      - NITENS (SANDER'S)
        - INSIGNE — NEUROPETALUM
        - VILLOSUM — NEUROPETALUM

14. X EARL OF CHESTER = SUNSET. EARL OF CHESTER (6 / 0)
    - BINGLEYENSE (CHORLTONII)
      - CHARLESWORTHII — NEUROPETALUM
      - HARRISIANUM
        - BARBATUM — PHACOPETALUM
        - VILLOSUM — NEUROPETALUM
    - LORD ROBERTS
      - CHARLESWORTHII — NEUROPETALUM
      - CREON
        - HARRISIANUM
          - BARBATUM — PHACOPETALUM
          - VILLOSUM — NEUROPETALUM
        - CENANTHUM ?


15. X EMERALD = VERT. EMERALD
7 0
CURTISII (SANDERAE) — PHACOPETALUM
MAUDIAE
CALLOSUM VAR. SANDERAE — PHACOPETALUM
LAWRENCEANUM VAR. HYEANUM — PHACOPETALUM
16. X ENCHANTRESS = ESMERALDA. ENCHANTRESS
4 0
ALMA GAVAERT
MAUDIAE
CALLOSUM VAR. SANDERAE — PHACOPETALUM
LAWRENCEANUM VAR. HYEANUM — PHACOPETALUM
LAWRENCEANUM VAR. HYEANUM — PHACOPETALUM
CURTISII (SANDERAE) — PHACOPETALUM
17. X FAIRRIEANUM = FAIRE-MAUD. FAIRRIEANUM (SP.)
85 0
CERATOPETALUM
18. X FULMINISTER = PADDINGTON
2 0
FULMINISTER
FULMER
CHLORIS
LORD WOLMER
HERA
VILLOSUM VAR. BOXALLII — NEUROPETALUM
LEEANUM
INSIGNE — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
LEEANUM
INSIGNE — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
MRS. HILARY JENKINSON
? ?
PERSEUS
ALCIBIADES (ILLUSTRIOUS)
LEEANUM (GIGANTEUM)
INSIGNE — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
MONS. DE CURTE
INSIGNE — NEUROPETALUM
VILLOSUM VAR. BOXALLII — NEUROPETALUM
LADY DILLON
MRS. WM. MOSTYN (CHAROWAR)
HERA
VILLOSUM VAR. BOXALLII — NEUROPETALUM
LEEANUM
INSIGNE — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
?
NITENS (SALLIERI-AUREUM)
NITENS SALLIERI
INSIGNE — NEUROPETALUM
VILLOSUM — NEUROPETALUM
AUREUM
SPICERIANUM — CYMATOPETALUM
NITENS
INSIGNE — NEUROPETALUM
VILLOSUM — NEUROPETALUM
WESTMINSTER
ALCIBIADES
LEEANUM (GIGANTEUM)
INSIGNE — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
MONS. DE CURTE
INSIGNE — NEUROPETALUM
VILLOSUM VAR. BOXALLII — NEUROPETALUM
CHLORIS
LORD WOLMER
HERA
VILLOSUM VAR. BOXALLII — NEUROPETALUM
LEEANUM
INSIGNE — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
LEEANUM
INSIGNE — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
MRS. HILARY JENKINSON
? ?
19. X GOULTENIANUM = ONYX. GOULTENIANUM
6 0
CALLOSUM — PHACOPETALUM
CURTISII — PHACOPETALUM
20. X HOLDENII = WARDEN. HOLDENII
6 2
CALLOSUM VAR. SANDERAE — PHACOPETALUM
MAUDIAE
CALLOSUM VAR. SANDERAE — PHACOPETALUM
LAWRENCEANUM VAR. HYEANUM — PHACOPETALUM
21. X INSIGNE = ROSSETTI. INSIGNE (SP.)
148 6
NEUROPETALUM
22. X LAWRENCEANUM = ALMA GAVAERT. LAWRENCEANUM (SP.)
62 11
PHACOPETALUM
23. X LEEANUM = HANBURYANUM. LEEANUM
131 6
INSIGNE — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
24. X MRS. ELEY = ALDWITH M. BERRY. MRS. ELEY
43 0
CHRISTOPHER
ACTAEUS
INSIGNE — NEUROPETALUM
LEEANUM
INSIGNE — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
LEEANUM
INSIGNE — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
COMMODORE
ALCIBIADES
LEEANUM (GIGANTEUM)
INSIGNE — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
MONS. DE CURTE
INSIGNE — NEUROPETALUM
VILLOSUM VAR. BOXALLII — NEUROPETALUM
MEMORIA JERNINGHAMIAE
SPICERIANUM — CYMATOPETALUM
WINNIANUM
VILLOSUM — NEUROPETALUM
DRURYI — THIOPETALUM
25. X NIVEUM = PURITY. NIVEUM (SP.)
52 3
SUBGENUS BRACHYPETALUM

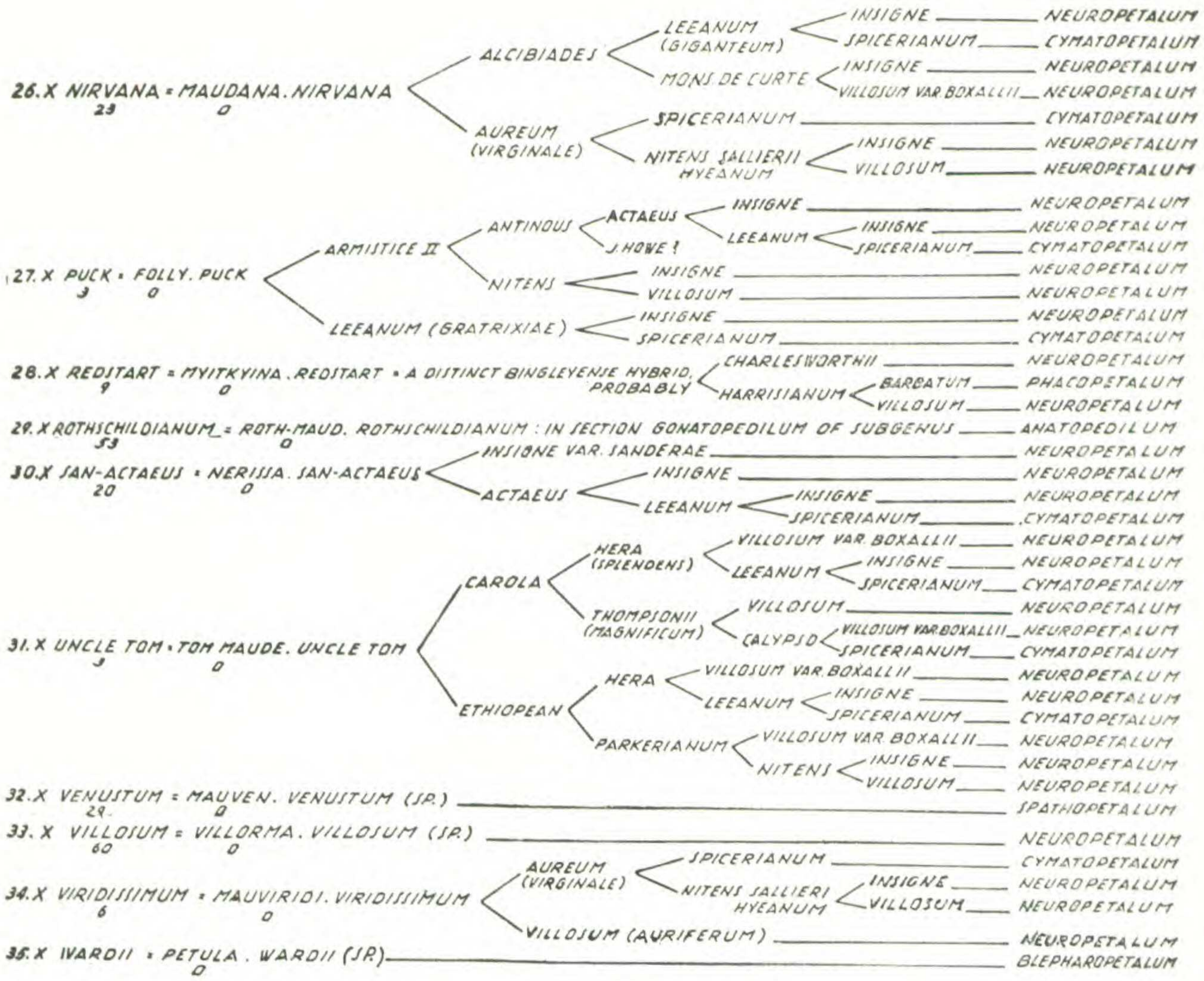

26. X NIRVANA = MAUDANA. NIRVANA
23 0
ALCIBIADES
LEEANUM (GIGANTEUM)
INSIGNE — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
MONS. DE CURTE
INSIGNE — NEUROPETALUM
VILLOSUM VAR. BOXALLII — NEUROPETALUM
AUREUM (VIRGINALE)
SPICERIANUM — CYMATOPETALUM
NITENS SALLIERII HYEANUM
INSIGNE — NEUROPETALUM
VILLOSUM — NEUROPETALUM
27. X PUCK = FOLLY. PUCK
3 0
ARMISTICE II
ANTINOUS
ACTAEUS
INSIGNE — NEUROPETALUM
J. HOWE !
LEEANUM
INSIGNE — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
NITENS
INSIGNE — NEUROPETALUM
VILLOSUM — NEUROPETALUM
LEEANUM (GRATRIXIAE)
INSIGNE — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
28. X REDSTART = MYITKYINA . REDSTART = A DISTINCT BINGLEYENSE HYBRID, PROBABLY
9 0
CHARLESWORTHII — NEUROPETALUM
HARRISIANUM
BARBATUM — PHACOPETALUM
VILLOSUM — NEUROPETALUM
29. X ROTHSCHILDIANUM = ROTH-MAUD. ROTHSCHILDIANUM : IN SECTION GONATOPEDILUM OF SUBGENUS — ANATOPEDILUM
53 0
30. X SAN-ACTAEUS = NERISSA. SAN-ACTAEUS
20 0
INSIGNE VAR. SANDERAE — NEUROPETALUM
ACTAEUS
INSIGNE — NEUROPETALUM
LEEANUM
INSIGNE — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
31. X UNCLE TOM = TOM MAUDE. UNCLE TOM
3 0
CAROLA
HERA (SPLENDENS)
VILLOSUM VAR. BOXALLII — NEUROPETALUM
LEEANUM
INSIGNE — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
THOMPSONII (MAGNIFICUM)
VILLOSUM — NEUROPETALUM
CALYPSO
VILLOSUM VAR. BOXALLII — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
ETHIOPEAN
HERA
VILLOSUM VAR. BOXALLII — NEUROPETALUM
LEEANUM
INSIGNE — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
PARKERIANUM
VILLOSUM VAR. BOXALLII — NEUROPETALUM
NITENS
INSIGNE — NEUROPETALUM
VILLOSUM — NEUROPETALUM
32. X VENUSTUM = MAUVEN. VENUSTUM (JR.)
29 0
— SPATHOPETALUM
33. X VILLOSUM = VILLORMA. VILLOSUM (JR.)
60 0
— NEUROPETALUM
34. X VIRIDISSIMUM = MAUVIRIDI. VIRIDISSIMUM
6 0
AUREUM (VIRGINALE)
SPICERIANUM — CYMATOPETALUM
NITENS SALLIERI HYEANUM
INSIGNE — NEUROPETALUM
VILLOSUM — NEUROPETALUM
VILLOSUM (AURIFERUM) — NEUROPETALUM
35. X IVARDII = PETULA . WARDII (JR.)
0
— BLEPHAROPETALUM

CHART II

LIST OF CROSSES IN WHICH *P. CALLOSUM* HAS BEEN USED AS A PARENT

Section of OTOPEDILUM (or other subgenera) used in cross		Species or hybrid used as parent*		Resulting progeny	
1. PHACOPETALUM	×	ALMA GAVAERT (Chart I #2)†	11‡	NEREID	0‡
2. PHACOPETALUM NEUROPETALUM	×	APPLETONIANUM (App. Chart. II #1)	4	SIAMENSE	1
3. PHACOPETALUM	×	*Argus*	40	CALLOSO-ARGUS	0
4. PHACOPETALUM NEUROPETALUM	×	ASHBURTONIAE (App. Chart II #2)	12	ZENOBIA	1
5. NEUROPETALUM CYMATOPETALUM	×	AUREUM (Chart I #11)	58	ALTRICHAMENSE	0
6. PHACOPETALUM	×	*barbatum*	49	CALLOSO-BARBATUM	10
7. Subg. BRACHYPETALUM	×	*bellatulum*	57	WOTTONII	1
8. NEUROPETALUM	×	*Boxallii* (var. of sp. *villosum*)§	42	J. BARTELS	0
9. PHACOPETALUM Subg. ANATOPEDILUM Sect. CORYOPEDILUM	×	CALLO-ROTHSCHILDIANUM (App. Chart II #3)	1	FRANCONIA	0
10. PHACOPETALUM SPATHOPETALUM	×	CALOPHYLLUM (App. Chart II, #4)	13	PALLAS	2
11. COCHLOPETALUM	×	*Chamberlainianum*	38	ALCIPPE	0
12. NEUROPETALUM	×	*Charlesworthii*	66	ROSITA	0
13. PHACOPETALUM	×	*ciliolare*	27	ZEUS	0
14. Subg. BRACHYPETALUM	×	*concolor*	27	CONCO-CALLOSUS	0
15. PHACOPETALUM	×	*Curtisii*	44	GOULTENIANUM	6
16. Subg. BRACHYPETALUM	×	*Delenatii*	14	MME. MARTINET	1
17. THIOPETALUM	×	*Druryi*	33	A. R. SMITH	0
18. NEUROPETALUM	×	*exul*	20	DR. CONWAY	0
19. CERATOPETALUM	×	*Fairrieanum*	85	JUNO	1
20. PHACOPETALUM NEUROPETALUM	×	*gigas* (App. Chart II, #5)	8	E. J. SEYMOUR	0
21. Subg. BRACHYPETALUM	×	*Godefroyae*	31	FELIX FAURE	0
22. PHACOPETALUM	×	GOULTENIANUM (Chart II, #15)	6	MALHERBE	0
23. PHACOPETALUM	×	GOWERIANUM (App. to Chart II, #6)	19	HORTENSE	0
24. PHACOPETALUM NEUROPETALUM	×	HARRISIANUM (App. to Chart II, #1)	72	LEDOUXIAE	1
25. STICTOPETALUM	×	*hirsutissimum*	33	DONCASTERIANUM	0
26. NEUROPETALUM	×	HITCHINSIAE (App. to Chart II, #7)	17	SONIA	0
27. PHACOPETALUM	×	HOLDENII (Chart II, #37)	6	GLORIOSUM	0
28. SPATHOPETALUM	×	*Hookerae*	26	FORTUNA	0
29. NEUROPETALUM	×	*insigne*	148	LEONIAE	2
30. BLEPHAROPETALUM	×	*javanicum*	7	JAVA	0

*Species names are indicated in italics; hybrids, subgenera, and sections in caps.
†Key to explanations of varietal backgrounds are given in parentheses.
‡The figures following the names indicate the number of times the plant has been used in crosses.
§Treated as *P. villosum* var. *Boxallii* in Sander's 'Complete List of Orchid Hybrids'; treated as species *P. Boxallii* by G. A. L. Mehlquist (1947) and R. E. Duncan (1947).

Section of Otopedilum (or other subgenera) used in cross		Species or hybrid used as parent*		Resulting progeny	
31. Neuropetalum Cymatopetalum Subg. Brachypetalum	×	J. M. Black (App. Chart II, #8)	46	James	0
32. Cymatopetalum Neuropetalum	×	Lathamianum (App. Chart II, #9)	39	Calliope	0
33. Phacopetalum	×	*Lawrenceanum*	62	Maudiae	35
34. Neuropetalum Cymatopetalum	×	Leeanum (Chart I, #1)	132	Angeliae	0
35. ?	×	Madame Coffinet	2	Madam Maxine Opoix	0
36. Blepharopetalum	×	*Mastersianum*	24	Pytho	0
37. Phacopetalum	×	Maudiae (Chart I, #2)	35	Holdenii	6
38. Neuropetalum	×	nitens (Chart I, #3)	66	Wendigo	0
39. Subg. Brachypetalum	×	*niveum*	48	Winifred Hollington	1
40. Phacopetalum Neuropetalum	×	oenanthum (App. Chart III, #2)	28	Olga Bogshawe	0
41. Subg. Anatopedilum Sect. Coryopedilum	×	*phillippinense*	22	Millmanii	0
42. Subg. Anatopedilum Sect. Coryopedilum	×	*Rothschildianum*	53	callo-Roths-childianum	1
43. Subg. Anatopedilum Sect. Coryopedilum	×	*Sanderianum*	13	Princess May	0
44. Blepharopetalum	×	sementa (App. Chart II, #10)	8	Aurelianense	0
45. Cymatopetalum	×	*Spicerianum*	62	Mlle. Gabrielle Moens	0
46. Subg. Anatopedilum Sect. Prenipedilum	×	*Stonei*	27	Fordianum	0
47. Phacopetalum	×	*superbiens*	39	Moussetianum	0
48. Phacopetalum	×	superciliare (App. Chart II, #11)	18	Moreauanum	0
49. Phacopetalum Subg. Brachypetalum	×	Tautzianum (App. Chart II, #12)	2	Nandii	0
50. Blepharopetalum	×	*tonsum*	33	Felicity	0
51. Phacopetalum Neuropetalum	×	triumphans (App. Chart II, #13)	1	Rajah	0
52. Spathopetalum	×	*venustum*	29	Orpheus	3
53. Neuropetalum	×	*villosum*	60	Indra	0
54. Phacopetalum Blepharopetalum	×	William Matthews (App. Chart II, #14)	1	Ernest Read	2
55. Phacopetalum Subg. Brachypetalum	×	Winifred Hollington (App. Chart II, #15)	1	Winsum	0
					74

APPENDIX TO CHART II

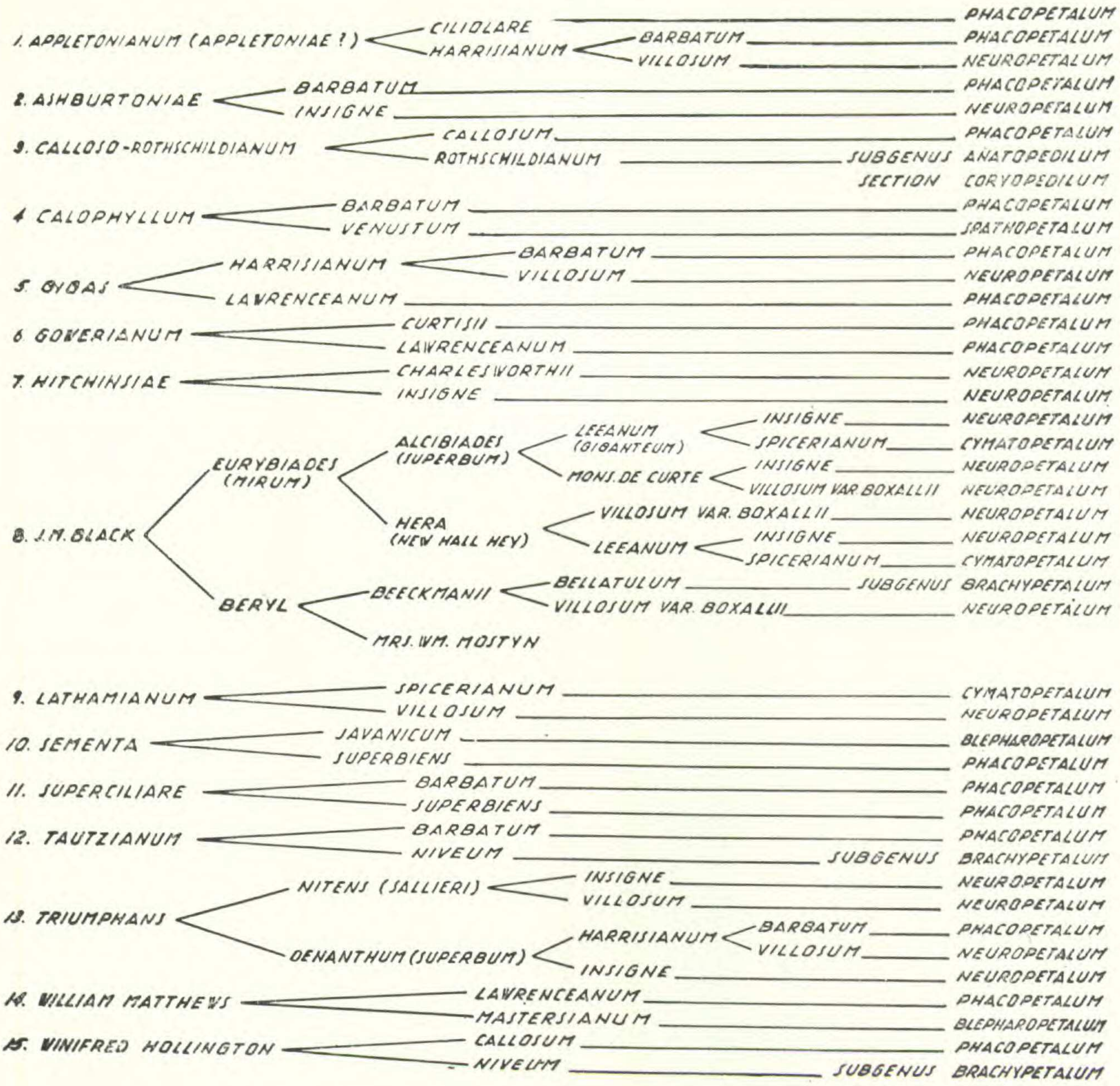


CHART III

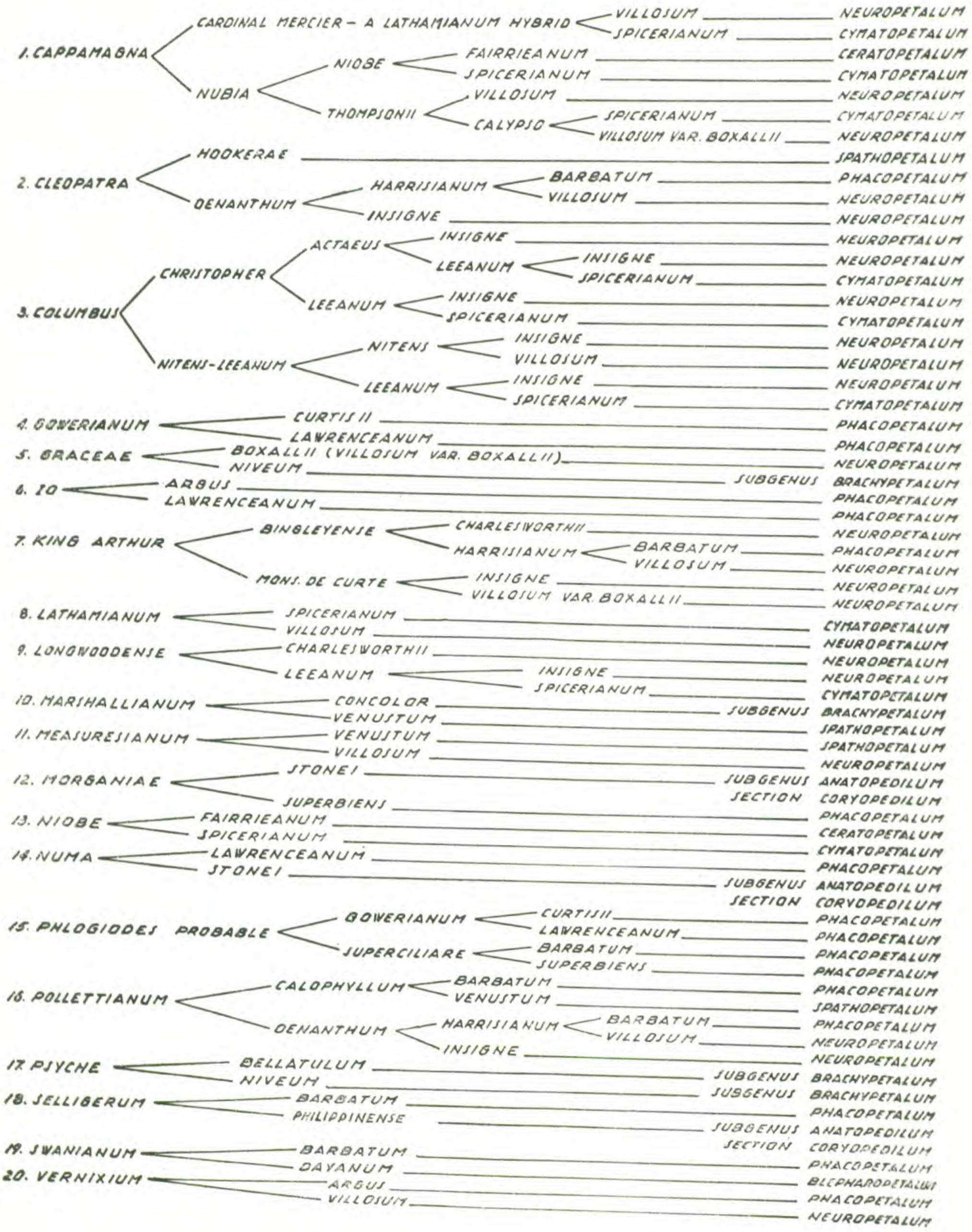
LIST OF CROSSES IN WHICH *P. LAWRENCEANUM* HAS BEEN USED AS A PARENT*

Section of Otopedilum (or other subgenera) used in cross		Species or hybrid used as parent		Resulting progeny	
1. Phacopetalum	×	Alma Gavaert (Chart I, #2)	11	Eleanor Rozilla	0
2. Phacopetalum	×	*Argus*	40	Io	15
3. Phacopetalum	×	*barbatum*	49	Almum	3
4. Subg. Brachypetalum	×	*bellatutum*	57	Laure-Bel	2
5. Neuropetalum	×	*villosum* var. *Boxallii*	42	Thayerianum	0
6. Phacopetalum	×	calloso-barbatum (Chart I, #6)	10	Myth	0
7. Phacopetalum	×	*callosum*	55	Maudiae	35
8. Neuropetalum Cymatopetalum Ceratopetalum	×	cappamagna (App. to Chart III, #1)	46	Montrose	0
9. Cochlopetalum	×	*Chamberlainianum*	38	Hiero	0
10. Neuropetalum	×	*Charlesworthii*	66	decipiens	0
11. Phacopetalum	×	*ciliolare*	27	Smithii	4
12. Spathopetalum Phacopetalum Neuropetalum	×	Cleopatra (App. to Chart III, #2)	1	resplendens	0
13. Neuropetalum Cymatopetalum	×	Columbus (App. to Chart II, #3)	11	Sardow	0
14. Subg. Brachypetalum	×	*concolor*	27	Conco-Laure	0
15. Phacopetalum	×	*Curtisii*	44	Gowerianum	19
16. Blepharopetalum	×	*Dayanum*	26	Littleanum	0
17. Thiopetalum	×	*Druryi*	33	Cybele	0
18. Neuropetalum	×	*exul*	20	Julia	0
19. Ceratopetalum	×	*Fairrieanum*	85	Streathamense	0
20. Subg. Brachypetalum	×	*Godefroyae*	31	Don Carlos	0
21. Phacopetalum	×	Gowerianum (App. Chart II, #6)	19	Laure-Gower	0
22. Neuropetalum Subg. Brachypetalum	×	Graceae (App. Chart III, #5)	2	Grigna	0
23. Phacopetalum Neuropetalum	×	Harrisianum (App. to Chart III, #2)	72	gigas	8
24. Stictopetalum	×	*hirsutissimum*	33	Mulas	0
25. Phacopetalum	×	Holdenii (Chart I, #20)	6	Pauliae	0
26. Spathopetalum	×	*Hookerae*	26	Enfieldense	2
27. Neuropetalum	×	*insigne*	148	Umlauftianum	0
28. Phacopetalum	×	Io (App. to Chart III, #6)	15	Vanninii	0
29. Neuropetalum Phacopetalum	×	King Arthur (App. Chart III, #7)	9	Erl King	0
30. Cymatopetalum Neuropetalum	×	Lathamianum (App. Chart II, #9)	39	Pynaertii	0
31. Neuropetalum Cymatopetalum	×	Leeanum (App. Chart III, #3)	132	Magnei	0
32. Neuropetalum Cymatopetalum	×	Longwoodense (App. Chart III, #9)	18	Venizelos	0

*See footnotes Chart II for explanation.

Section of OTOPEDILUM (or other subgenera) used in cross		Species or hybrid used as parent		Resulting progeny	
33. PARDALOPETALUM	×	*Lowii*	20	MACFARLANIANUM (If Macfarlanei = 1)	0
34. ?	×	L'YSER	6	ALAIN GERBAULT	6
35. BLEPHAROPETALUM	×	*Mastersianum*	24	WILLIAM MATTHEWS	1
36. Subg. BRACHYPETALUM SPATHOPETALUM	×	MARSHALLIANUM (App. Chart III, #10)	1	HENRY GRAVES	0
37. PHACOPETALUM	×	MAUDIAE (Chart I, #2)	35	ALMA GAVAERT	11
38. SPATHOPETALUM NEUROPETALUM	×	MEASURESIANUM (App. Chart III, #11)	4	HEBE	0
39. Subg. ANATOPEDILUM Sect. CORYOPEDILUM PHACOPETALUM	×	MORGANIAE (App. Chart III, #12)	11	VENETIA	0
40. CERATOPETALUM CYMATOPETALUM	×	NIOBE (App. Chart III, #13)	28	WELLESLEYI	2
41. NEUROPETALUM	×	NITENS (Chart I, #3)	66	JOHNSONIANUM	0
42. Subg. BRACHYPETALUM	×	*niveum*	48	ANTIGONE	2
43. PHACOPETALUM Subg. ANATOPEDILUM Sect. CORYOPEDILUM	×	NUMA (App. Chart III, #14)	2	STANDENSE	0
44. PHACOPETALUM NEUROPETALUM	×	OENANTHUM (App. Chart III, #2)	28	BIJOU	0
45. MYSTROPEDILUM	×	*Parishii*	5	ELIZABETHAE	0
46. Subg. ANATOPEDILUM Sect. CORYOPEDILUM	×	*philippinense*	22	CHARLES STEINMETZ	0
47. PHACOPETALUM	×	PHLOGIODES (App. Chart III, #15)	1	NIGRUM	0
48. PHACOPETALUM SPATHOPETALUM NEUROPETALUM	×	POLLETTIANUM (App. Chart III, #16)	7	FABIA	0
49. Subg. BRACHYPETALUM	×	PSYCHE (App. Chart III, #17)	15	CONOPUS	0
50. Subg. ANATOPEDILUM Sect. GONATOPEDILUM	×	*Rothschildianum*	53	WIERTZIANUM	0
51. Subg. ANATOPEDILUM Sect. CORYOPEDILUM	×	*Sanderianum*	13	ULTOR	0
52. PHACOPETALUM Subg. ANATOPEDILUM Sect. CORYOPEDILUM	×	SELLIGERUM (App. Chart III, #18)	21	LADY LLANGATTOCK	0
53. BLEPHAROPETALUM PHACOPETALUM	×	SEMENTA (App. Chart II, #10)	8	CRASSIFOLIUM	0
54. CYMATOPETALUM	×	*Spicerianum*	62	RADIOSUM	2
55. Subg. ANATOPEDILUM Sect. CORYOPEDILUM	×	*Stonei*	27	NUMA	2
56. PHACOPETALUM	×	*superbiens*	39	EURYALE	5
57. PHACOPETALUM	×	SUPERCILIARE (App. Chart III, #15)	18	AUGUSTUM	2
58. PHACOPETALUM BLEPHAROPETALUM	×	SWANIANUM (App. Chart III, #19)	13	ROGERSII	0
59. BLEPHAROPETALUM	×	*tonsum*	33	MADAM BARBEY	0
60. SPATHOPETALUM	×	*venustum*	29	AUROREUM	2
61. PHACOPETALUM NEUROPETALUM	×	VERNIXIUM (App. Chart III, #20)	5	JULIEN COFFIGNIEZ	0
62. NEUROPETALUM	×	*villosum*	60	LURIDUM	0
					123

APPENDIX TO CHART III



Explanation of Plate

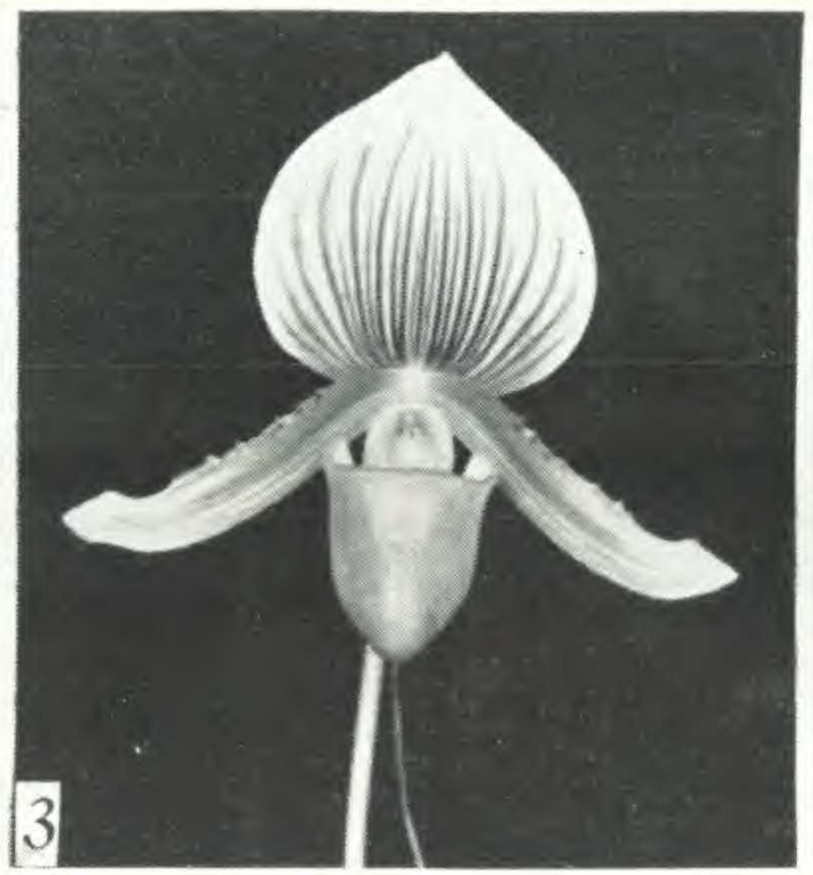
PLATE 31

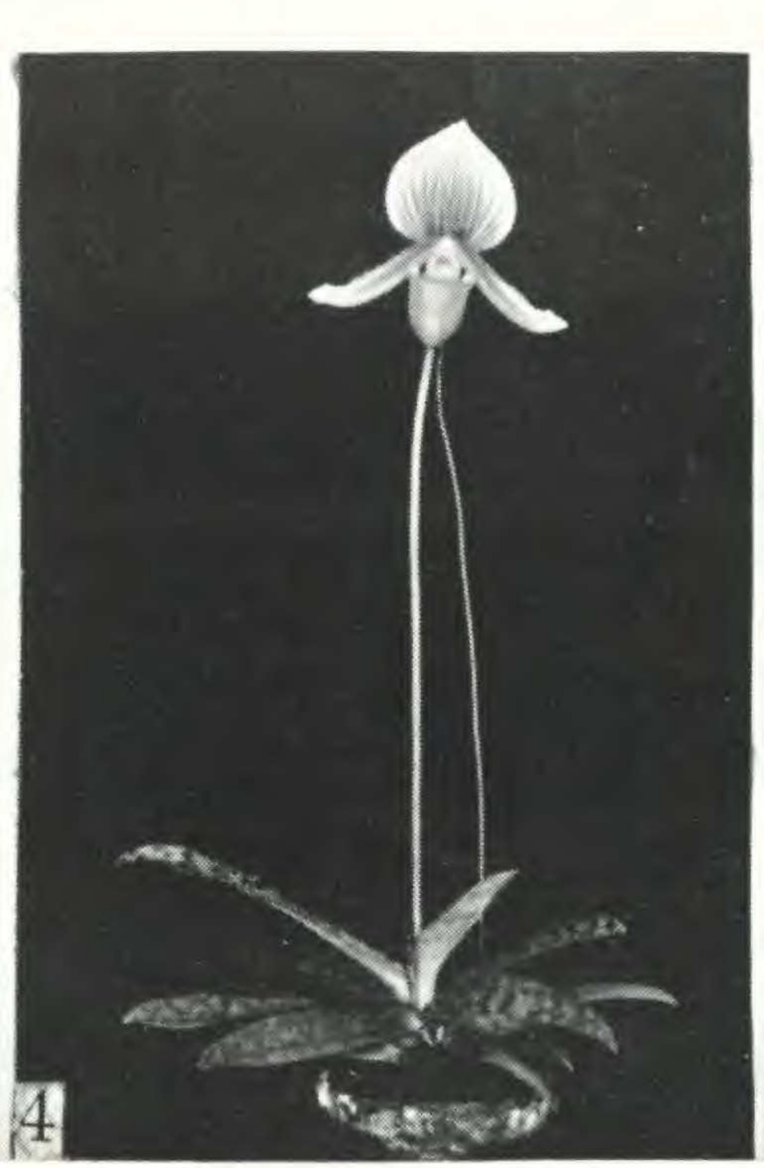
Flowers about ½; habits about ¼.

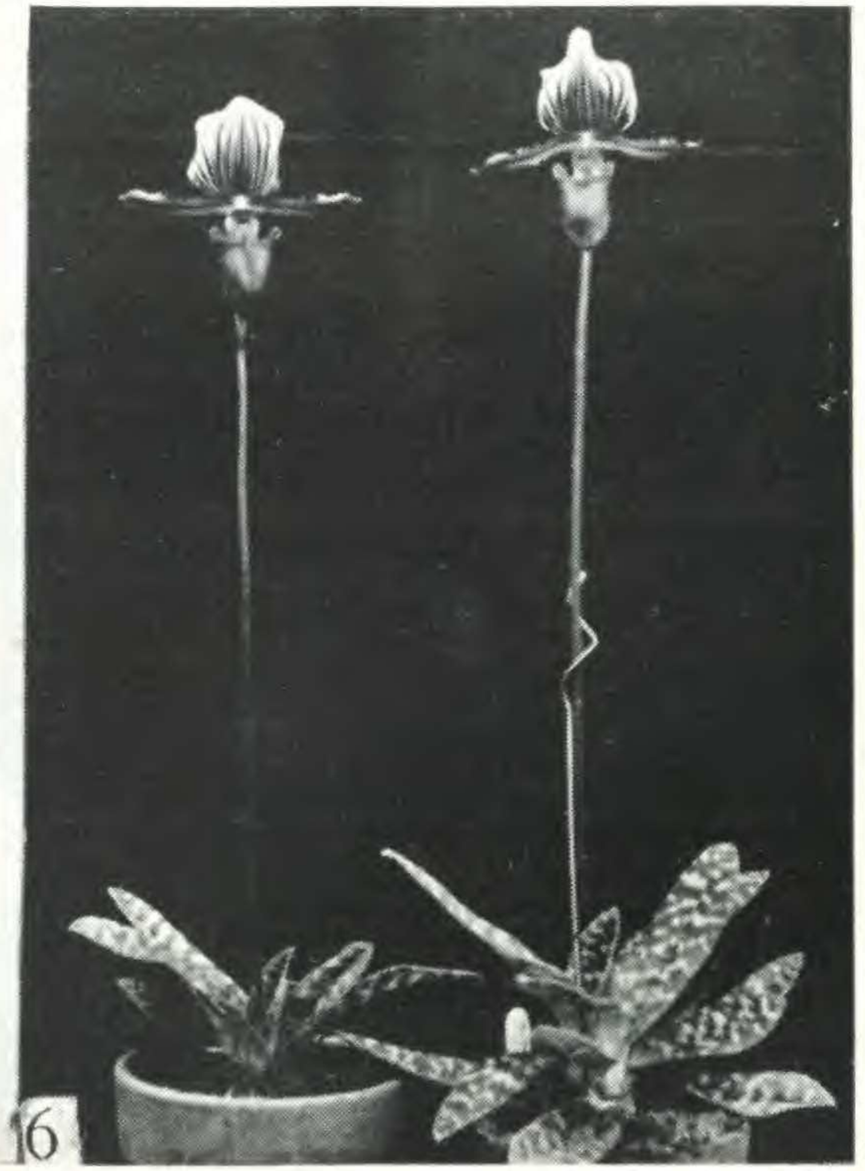
Figs. 1 and 2. *Paphiopedilum callosum.*

Figs. 3 and 4. *Paphiopedilum Maudiae* var. *magnificum.*

Figs. 5 and 6. *Paphiopedilum Lawrenceanum.*







McQUADE—*PAPHIOPEDILUM MAUDIAE* HORT.

Explanation of Plate

PLATE 32

A. Anaphase in root-tip of *Paphiopedilum callosum*, × 1350. Aceto-lacmoid.

B. Anaphase in root-tip of *P. Lawrenceanum*, × 1350. Feulgen.

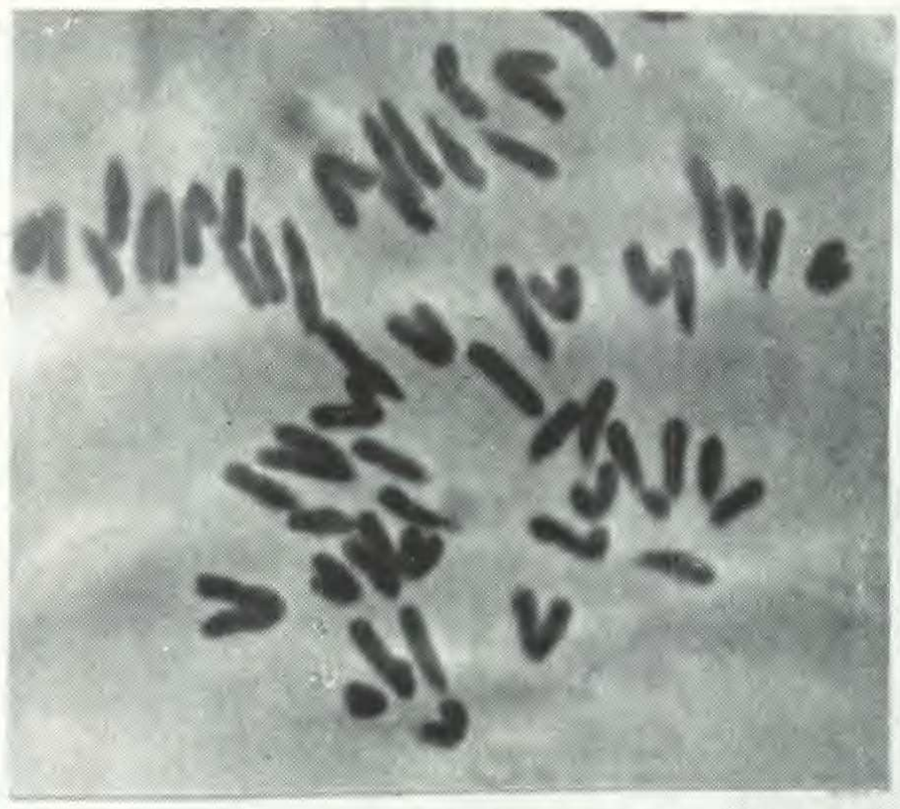
C. Metaphase of root-tip of *P. Maudiae*, × 1350. Feulgen. The two homologues showing the inversion are marked.

D. Camera-lucida drawing of the chromosome pair showing an apparently terminal inversion. These chromosomes are of intermediate length and have a prominent secondary constriction. The centromere is subterminal in one and median in the other (centromere marked with a line). Magnification × about 1800.

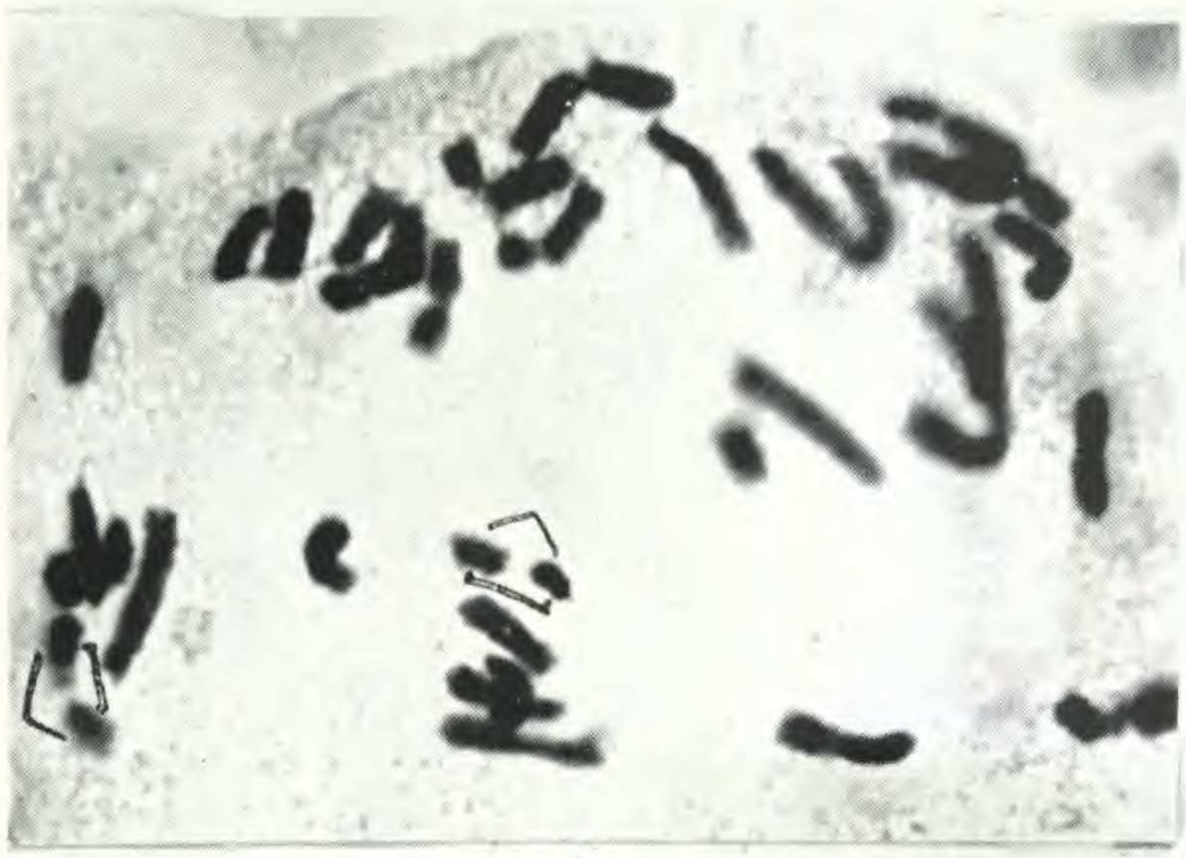
E. *P. callosum*. Metaphase I, 16 bivalents, × 1350. Crystal violet and safranin.

F. *P. Lawrenceanum*. Metaphase II, 18 chromosomes, × 1350. Crystal violet and safranin.

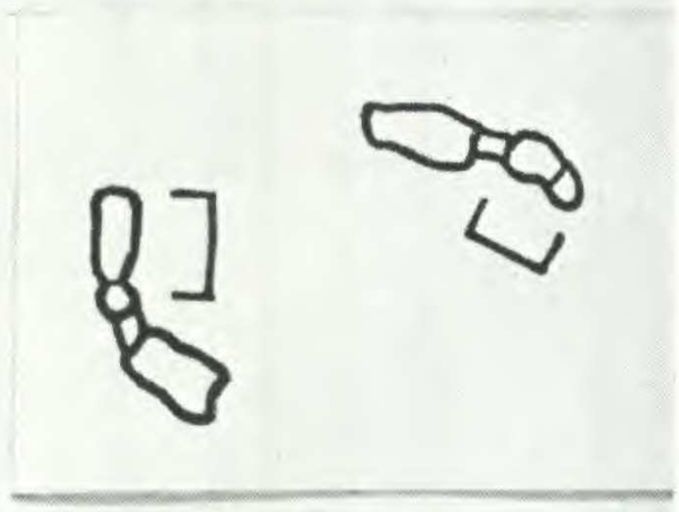
A



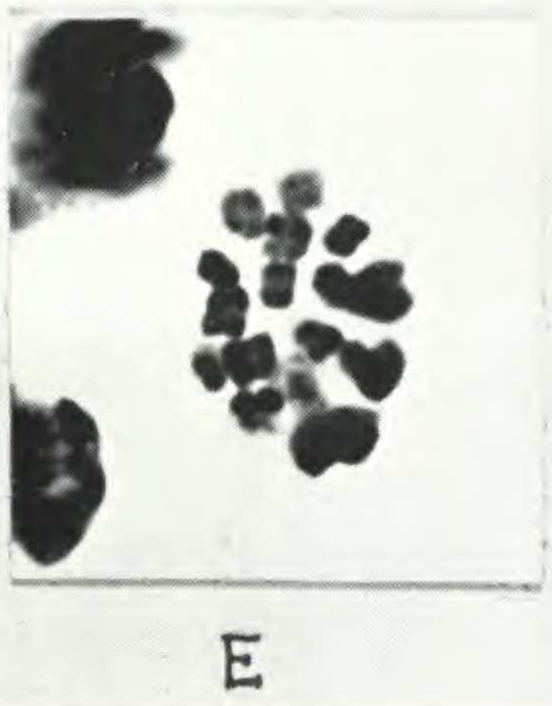
B



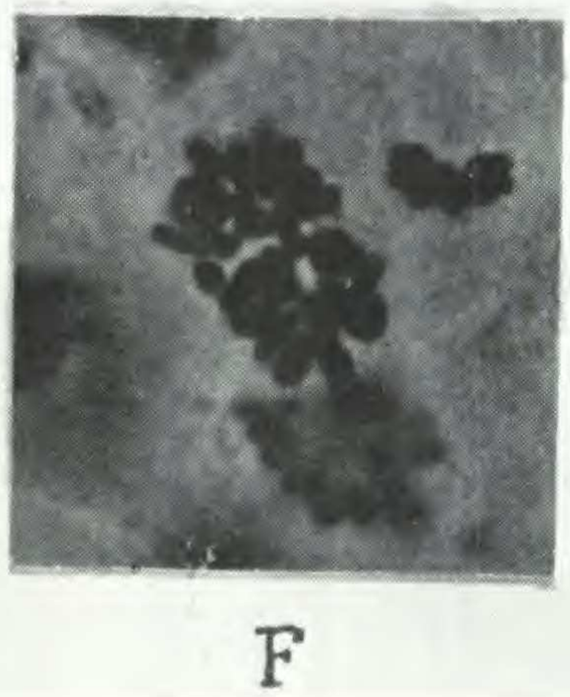
C



D



E



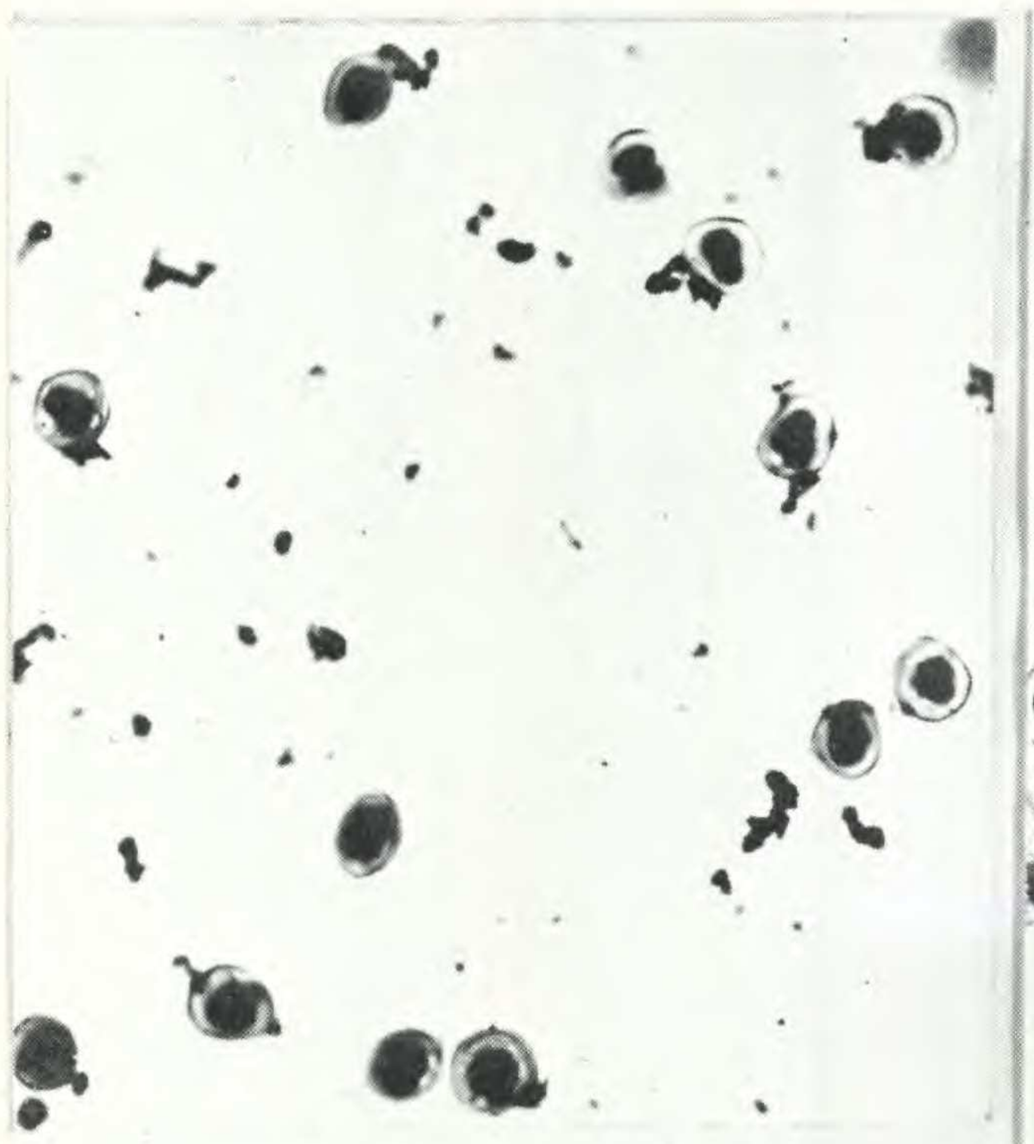
F

McQUADE—*PAPHIOPEDILUM MAUDIAE* HORT.

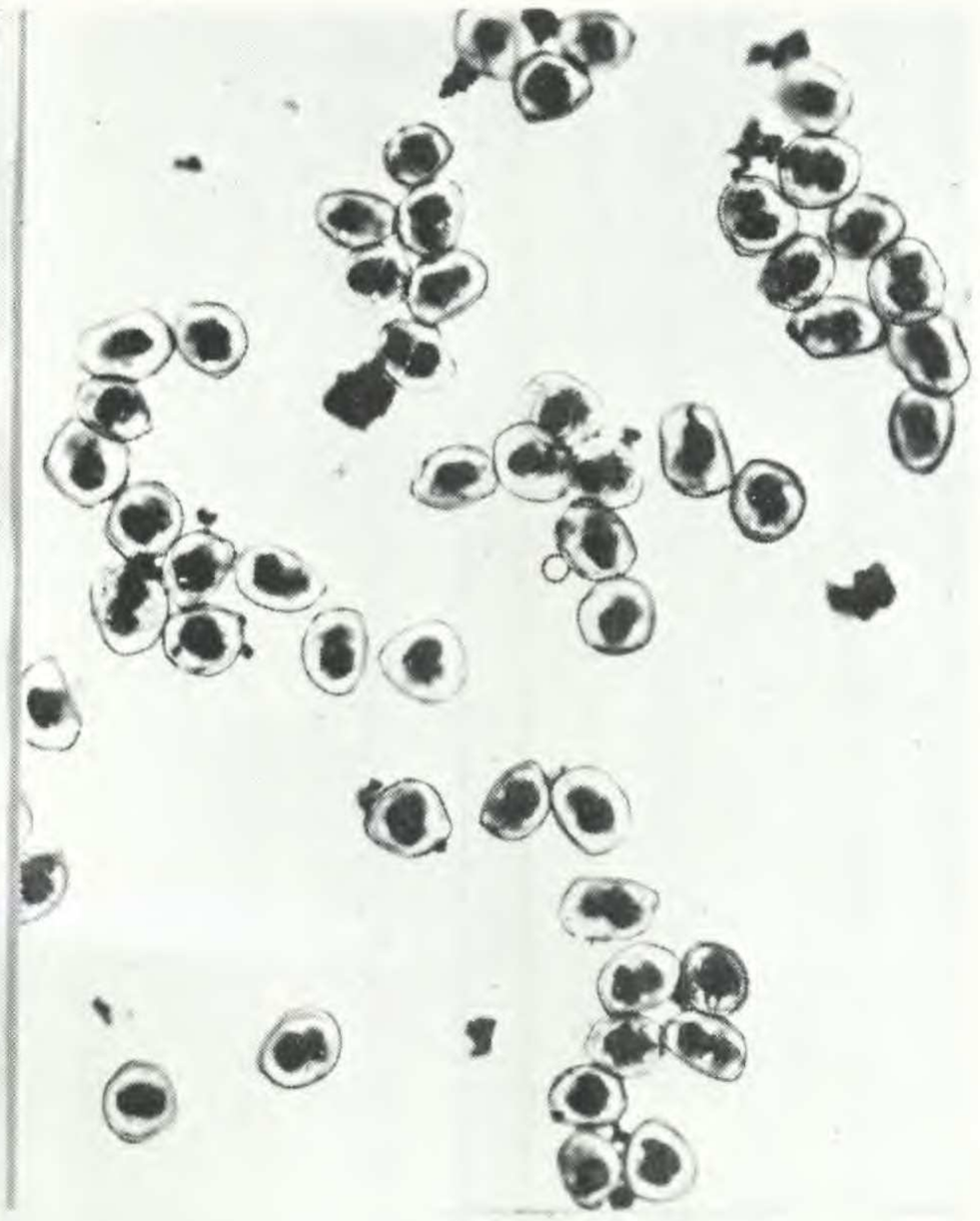
Explanation of Plate

PLATE 33

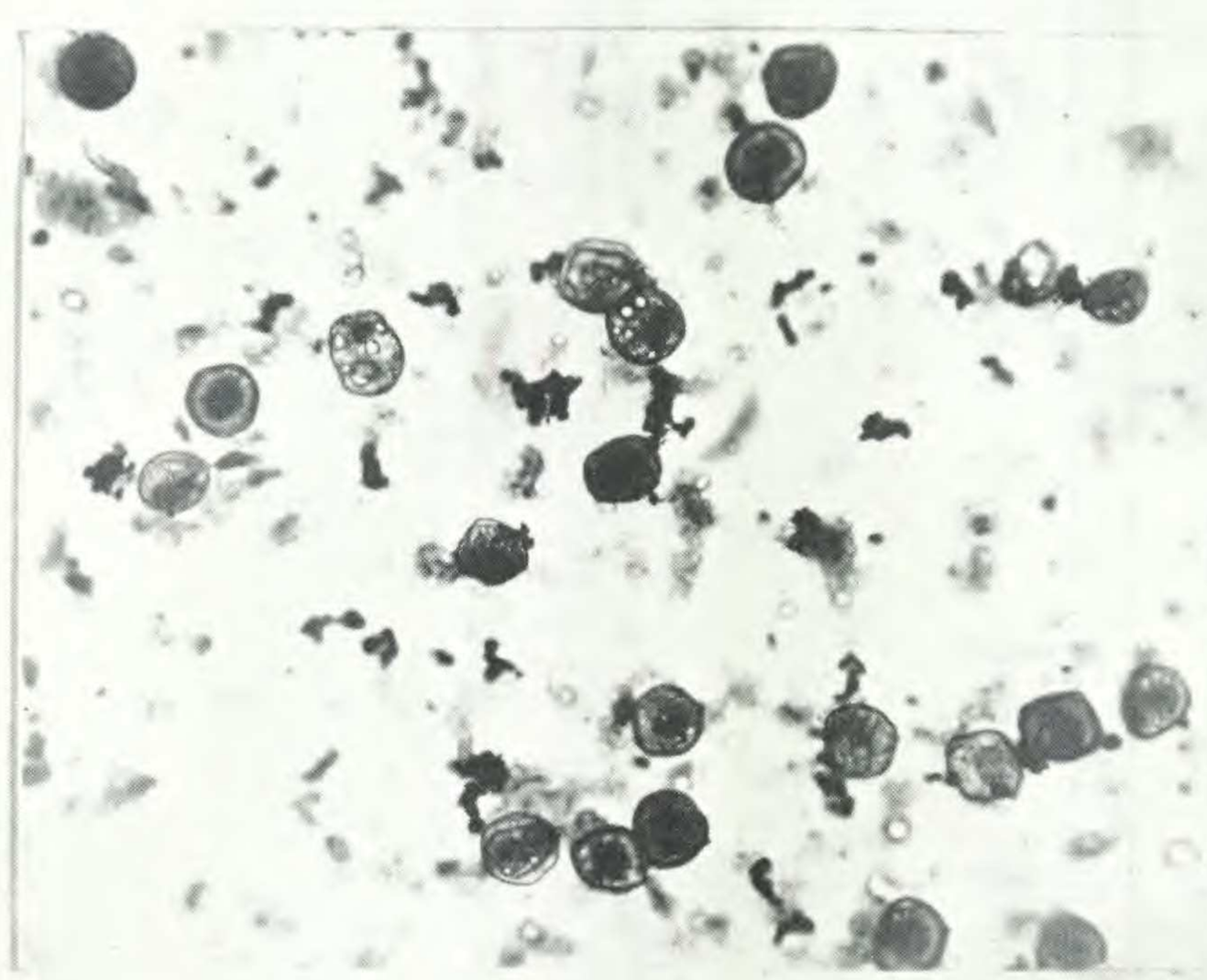
Pollen of *Paphiopedilum callosum*, of *P. Lawrenceanum*, and of *P. Maudiae*, × about 250.



P. callosum



P. Lawrenceanum



P. Maudiae

Explanation of Plate

PLATE 34

Paphiopedilum Maudiae Hort.

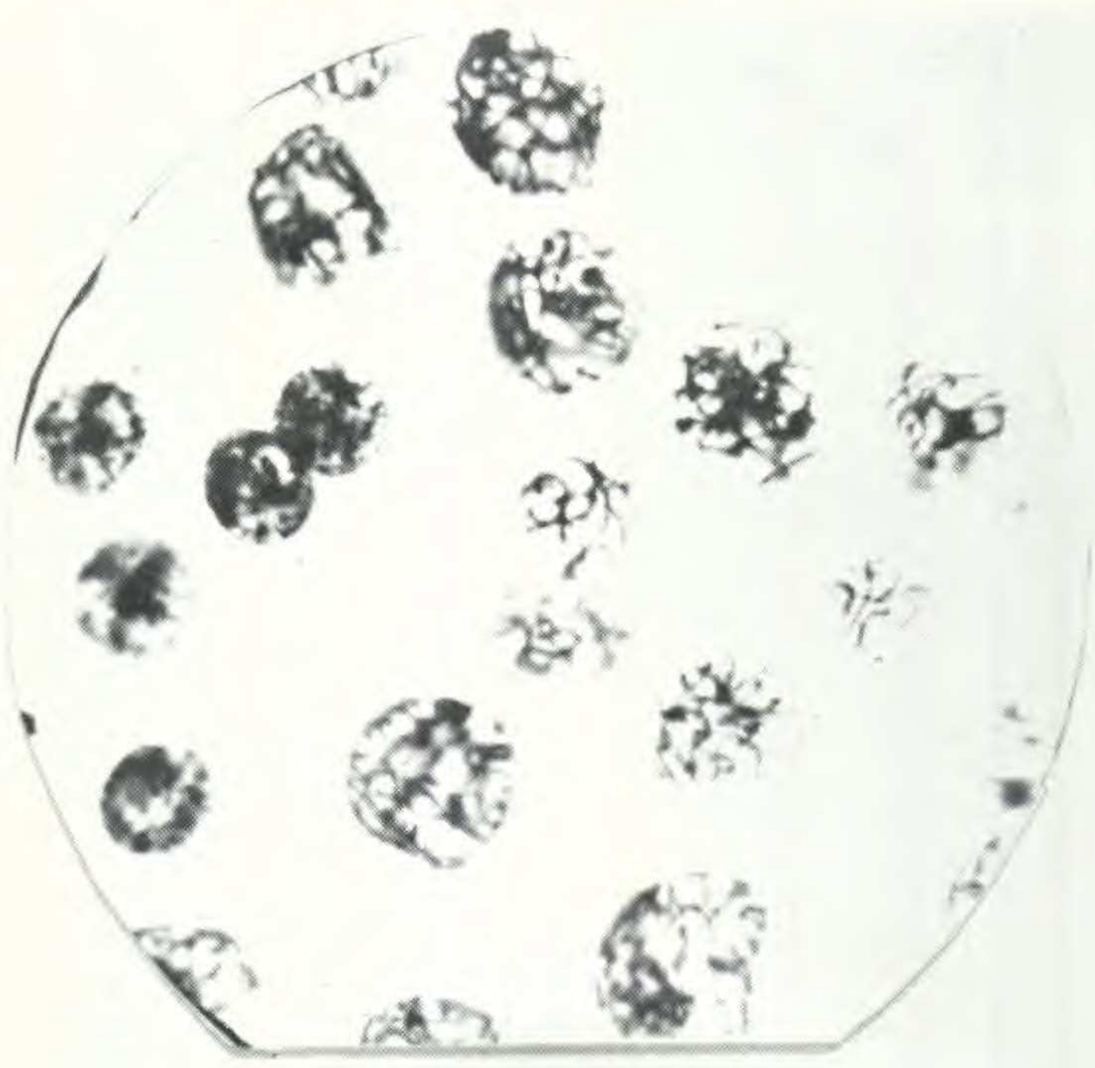
A. Pachytene-early diplotene, × about 1350.

B. Metaphase I, 17 bivalents, × about 650.

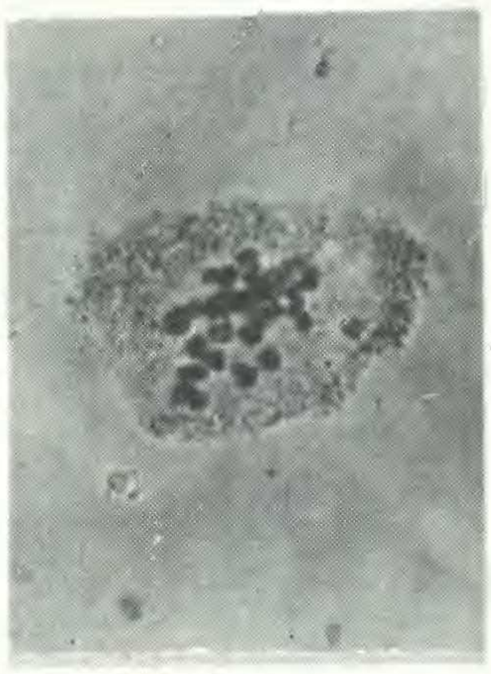
C. Anaphase I, bridge and fragment, × about 650.

D. Metaphase II, × about 750.

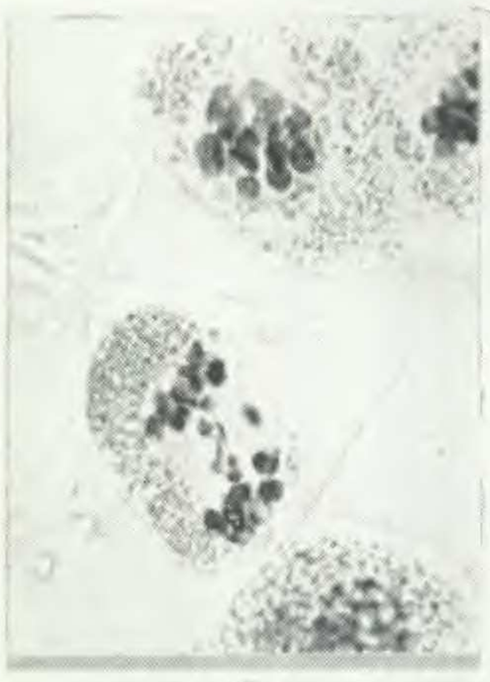
E. Tetrads (note micro-grain), × about 700.



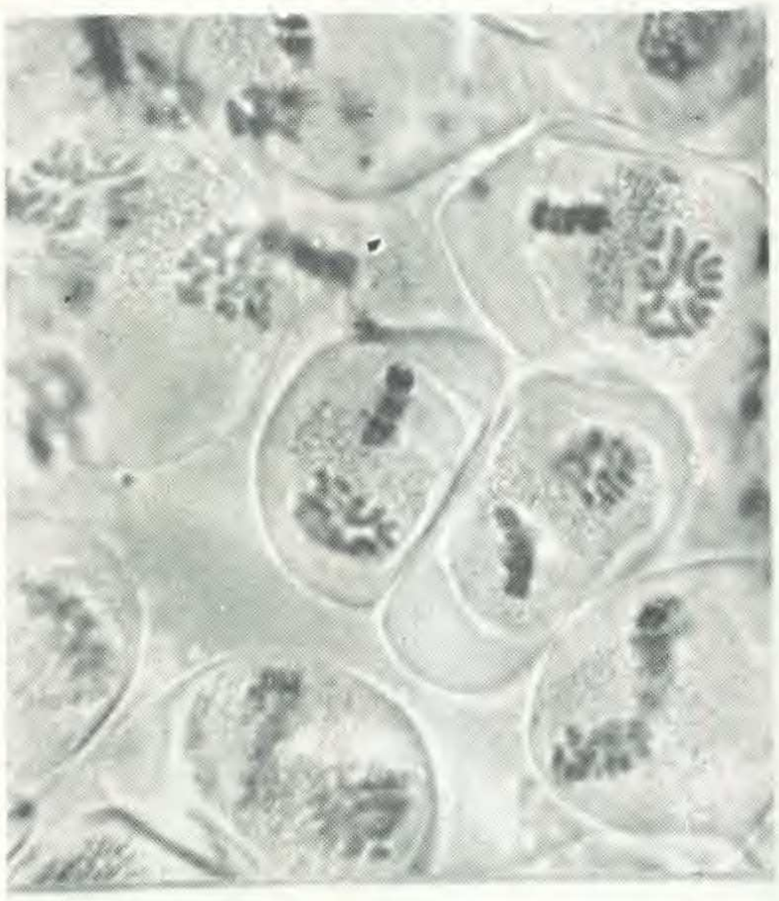
A



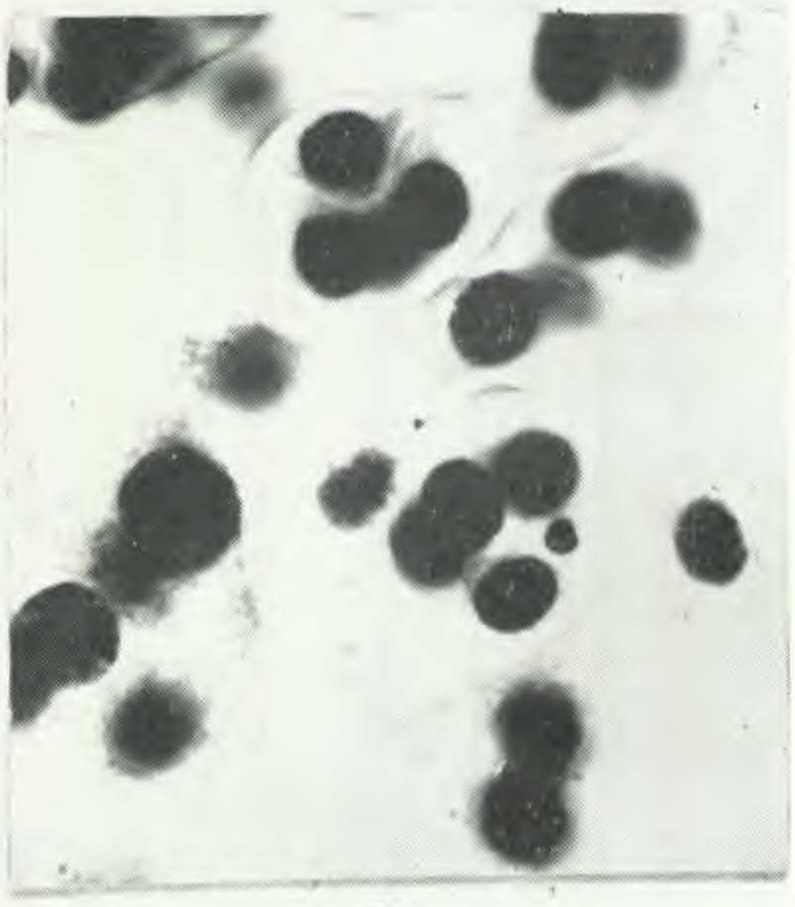
B



C



D



E

McQUADE—*PAPHIOPEDILUM MAUDIAE* HORT.

STEGNOSPERMA: A NEW SPECIES AND A GENERIC COMMENTARY

DAVID J. ROGERS

The genus *Stegnosperma* (Phytolaccaceae) has been considered monotypic since Walter's treatment for Engler's 'Pflanzenreich'[1]. However, an examination of specimens in the major North American herbaria shows the inclusive species S. *halimifolium* Benth. of Walter to be rather heterogeneous. Actually, three species exist, two of which have been described and published, the third noted by S. Watson on an herbarium label but never published. A description of the third species is provided here and is named for Dr. Watson.

STEGNOSPERMA **Watsonii** D. J. Rogers, n. sp. Frutices aut scandentes aut crassi patulique 1–5 m. alti, 1–5 m. diam., cortice griseo vel rufo-brunneo. Folia anguste spathulata vel elliptica emarginata vel rotunda vel acuta 1.0–3.5 cm. longa 0.5–2.5 cm. lata, petiolo 0.1–0.3 cm. longo. Inflorescentia cymulis axillaribus aut terminalibus 1–8-floris; calycis lobis ellipticis vel ovatis 0.3–0.7 cm. longis 0.2–0.4 cm. latis; petalis ovatis rotundatis basi abrupte constrictis; fructu capsula 5-loculata plerumque in 5 valvis dehiscente; seminibus plerumque 5 aliquando 4 ovoideis vel ellipsoideis circa 0.3 cm. longis 0.2–0.3 cm. latis, cicatrice funiculari laterali, raphe in jugum dorsalem, testa levi fulgenti rufo-brunneo.

Sprawling vine or coarse spreading shrub, 1–5 m. tall, 1–5 m. diameter spread; bark gray to reddish brown. Leaves narrowly spathulate to elliptic, emarginate to rounded to acute, 1.0–3.5 cm. long, 0.5–2.5 cm. wide, petiole 0.1–0.3 cm. long. Inflorescence of axillary or terminal 1- to 8-flowered cymules; calyx lobes elliptic to ovate, 0.3–0.7 cm. long, 0.2–0.4 cm. wide; petals ovate, rounded, abruptly constricted at base; fruit a 5-celled capsule, usually dehiscing by 5 valves; seeds usually 5, occasionally 4, ovoid to ellipsoid, about 0.3 cm. long, 0.2–0.3 cm. wide, funicular scar lateral, raphe on a dorsal ridge, testa smooth, shiny, reddish brown.

MEXICO: BAJA CALIFORNIA: *Wiggins 7681.* SINALOA: *Jones s. n.* SONORA: *Abrams 13343; Coville 1646; Dawson 1058; Drouet, Richards & Alvarado 3443; Ferris 8741; Gentry 2195, 2975; Goldman 399; Keck 4067; LeRoy s. n.; Lumholtz 9; McGee s. n.; William Palmer 1226* (HOLOTYPE in Herb. Missouri Botanical Garden, isotypes in Herb. N. Y. Bot. Gard. and U. S. Nat. Herb.); *Pringle s. n.; Rose 1211, 1211a; Rose, Standley & Russell 12390, 12566, 13138, 13231, 15047; Shreve 5992; Wiggins 6247.*

This species seems to be most closely related to S. *halimifolium* Benth., from which it may be distinguished by its scattered, few-flowered cymules, its ovate, abruptly constricted petals, and by its lateral funicular scar.

Stegnosperma Watsonii grows on hillsides along rivers, thickets in palm groves, thorny foothills, from sea level to 300 meters. It flowers from about the first of February through March, and fruits from the last of February through April.

That there are actually three species of *Stegnosperma* is most easily demonstrated by the following key:

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[1] Walter in Engl. Pflanzenr. IV, 83:124. 1909.

Issued November 30, 1949.